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The ecology of nest predation by red foxes Vulpes vulpes.

THE ECOLOGY OF NEST PREDATION BY RED FOXES *VULPES VULPES*

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A thesis submitted to the University of Bristol in accordance with the requirements for the degree of Doctor of Philosophy in the Faculty of Science

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Abstract

1. Although evidence for the impact of foxes on waterfowl and game bird nest success is common in the literature, there were very few measures of the impact of foxes *Vulpes vulpes* on waders and ground-nesting passerines. The mean Mayfield estimate (± s.d.) from nine independent measures of wader nest predation by foxes is 20.4 ± 22.3%. Data from a single study site shows that foxes may take 34% or more nests of shrubbsteppe passerines.
2. Lapwings *Vanellus vanellus* nesting at a site in northern England where foxes were known to be active, lost 30% of nests (n = 116) to predators. The daily probability of nest predation decreased significantly as the number of nearest neighbouring nests increased, a pattern thought to be brought about by crow *Corvus corone* predation.
3. During 200 hours of nocturnal observation at lapwing nesting sites, red foxes were shown to elicit 73% of nocturnal alarm calls by lapwings. The mean fox stay time was 641 ± 489 seconds (n = 17 visits). The duration of lapwing alarm calls elicited by foxes increased significantly with the minimum number of lapwing broods present at the site. The total fox stay time throughout the nesting season per hour of observation, and corrected for site area, was greater at sites with higher densities of nesting waterfowl.
4. Foxes were shown to initiate site-restricted search in the vicinity of lapwing broods and alarm calling adults on six occasions. Foxes were observed to carry out systematic search along linear habitats in a zigzag fashion.
5. The impact of nesting habitat area on the rate of nest predation was explored using a computer model that simulated fox search behaviour. Reductions in the area of nesting habitat (search area) lead to large increases in predation risk. Nests situated in search areas of less than *ca.* 4 ha had a particularly low probability of survival, even if the predator spent little time searching. In larger habitats, the nest predation rate was sensitive to the assumptions of search behaviour. The implications for the management of nest predation is discussed.

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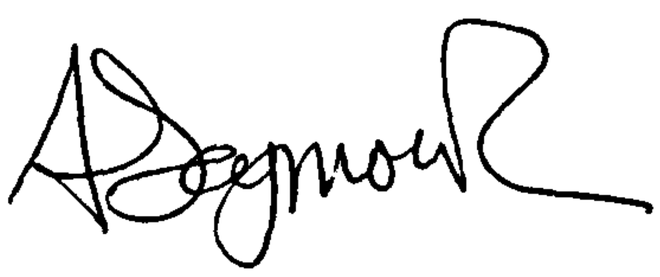
Declaration

I declare that the work in this dissertation was carried out in accordance with the regulations of the University of Bristol. Oliver Taylor assisted in the nocturnal observations of foxes in 1998. With this exception, I declare that the work in this thesis is my own and has not been submitted for any other degree or award. Any views expressed in the dissertation are my own and in no way represent those of the University of Bristol. The dissertation has not been presented to any other university for examination either in the United Kingdom or overseas.



Adrian Sean Seymour

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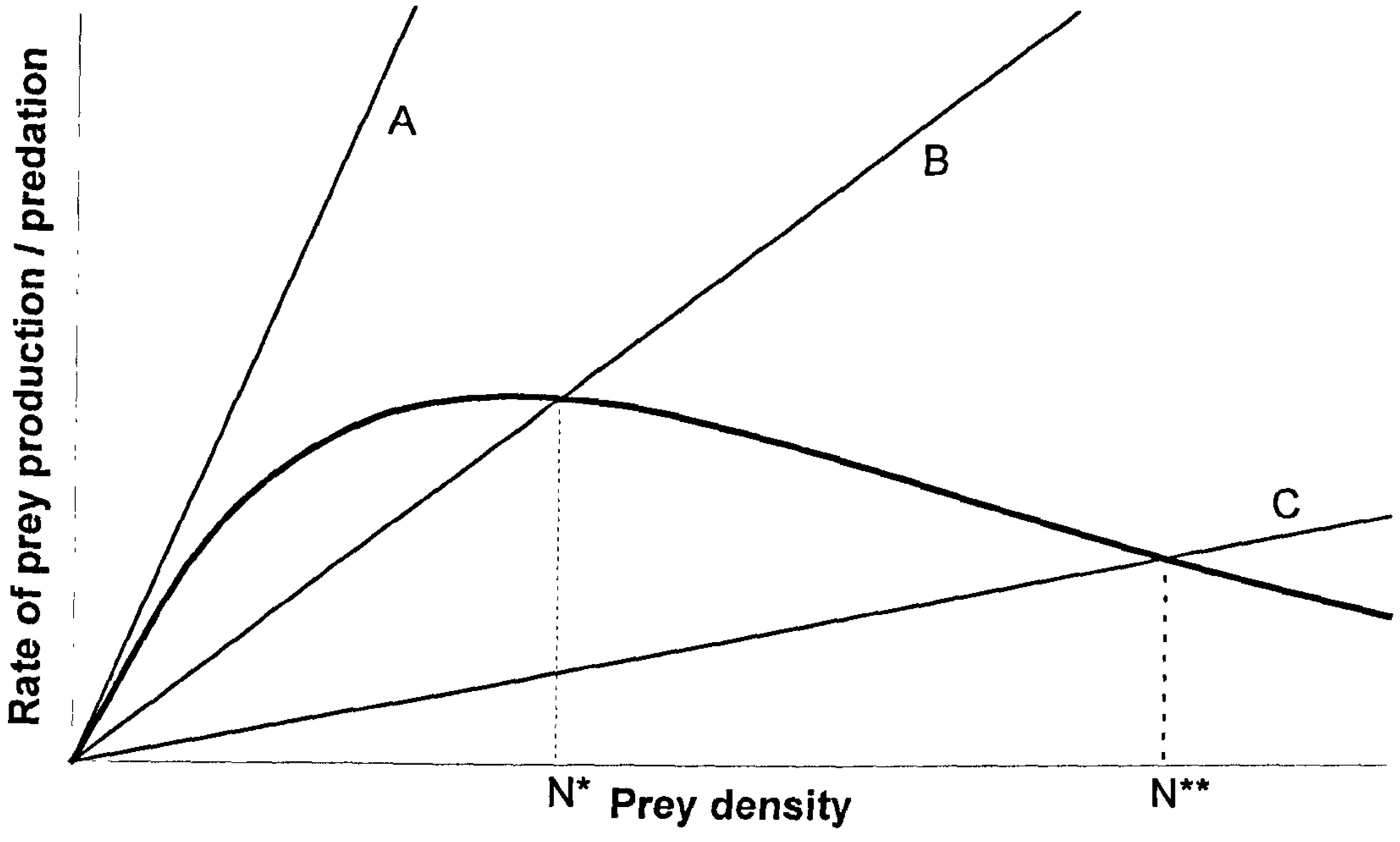
1. Introduction

1.1 The role of predation in the limitation and regulation of prey populations

All animal populations will have a limit to how large they can grow, because ultimately the heightened competition for the available resources will lead to increasing death rates and decreasing birth rates (Malthus, 1798; Nicholson, 1933). Although the availability of resources such as food and space will set the upper boundaries of population size, there are a number of other factors that may hold populations well below these limits. Weather and other environmental conditions can have a strong influence on mortality and productivity, and can potentially maintain numbers below a level enforced by resources (Andrewartha & Birch, 1954). Predation is another factor that has the potential to keep populations below their maximum potential size or carrying capacity (Sinclair, 1989; Crawley, 1992).

Figure 1.1 below shows how the productivity of an hypothetical prey population changes with prey density (thick line). At low densities the overall rate of productivity increases as the numbers of breeding individuals in the population increases. As the density of prey increases further, the rate of productivity drops as competition for limited resources intensifies. At the carrying capacity of the prey population the net rate of productivity will be zero. The rate of predation measured as the number of individuals consumed per unit time (thin lines) is assumed to increase at a constant rate so that the proportion of prey taken by predators remains constant regardless of prey density. When the rate of prey production equals the rate of predation the prey population will be at equilibrium. A predator with a high rate of consumption (line A) may drive its prey to extinction. Predators with lower consumption rates (lines B and C) may hold their prey populations at equilibria (N^* and N^{**}) below the carrying capacity of the population.

Figure 1.1 The effect of density independent predation on prey limitation. The thick line represents the prey production curve, the thin lines A, B and C represent prey consumption rates by predators with high, medium and low feeding rates respectively.



In the model populations shown in Figure 1.1 the prey population is limited by predation (lines B and C) but regulated by competition. Any process that regulates populations must have a density-dependent effect.

Predators can react to changes in prey numbers in a density-dependent fashion in two ways: 1) individuals can alter their feeding rate in response to prey density (the functional response) and 2) local predator populations can change in number in response to prey density (numerical response). Together, these two mechanisms determine the 'total response' of predators to prey density (Solomon, 1949; Holling, 1959). There are four types of functional response: the type-1 response shows a linear increase in feeding rate with prey density, typical of filter feeders; the type-2 functional response shows a decelerating increase in predation rate with prey density as the predator becomes satiated. The type-3 functional response has the greatest potential as a prey regulating behaviour,

with an accelerating phase of predation rate with increasing prey density followed by a decelerating increase in predation rate at higher prey densities. The accelerating phase in predation rate is linked to an increase in foraging efficiency by the predator, and the decelerating phase is related to predator satiation. The fourth type of functional response is characterised by a decreasing rate of predation at higher prey densities, brought about, for example, by increased anti-predator effects at high prey density.

Figure 1.2 The effect of a type-3 functional response on prey limitation and regulation. The thick line is the prey production curve, the thin sigmoid curve shows the change in a predator's feeding rate with prey density.

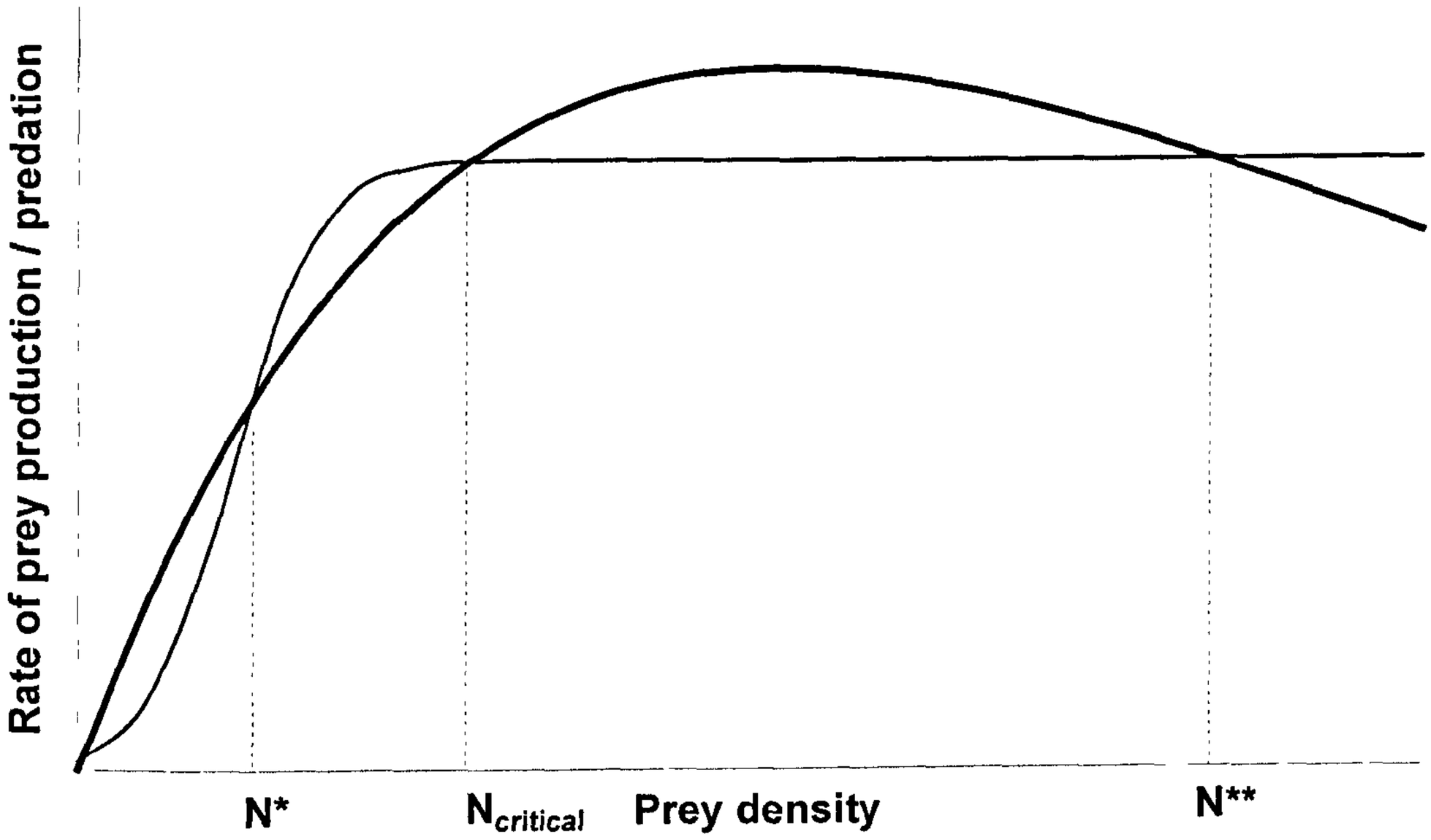


Figure 1.2 shows how a type-3 functional response can regulate a prey population. The thin sigmoid curve shows the rate of prey consumption, and the thick curve shows the rate of prey productivity or recruitment. When the prey population is greater then $N_{critical}$ it will reach an equilibrium N^{**}. If the prey density drops below $N_{critical}$ the prey will be regulated by predation and the prey population will converge on a new equilibrium N^{*}. If the equilibrium population experiences a perturbation to some level below $N_{critical}$, it will

return to N^*. The type-3 functional response may be a particularly important mechanism for prey regulation in predators that have a limited ability to respond numerically due to social constraints such as territoriality. The range of densities at which a prey population can be regulated by predators is termed a 'predator pit' or 'predator trap' (Sinclair, 1989).

Theoretically, predators can limit and regulate prey populations. In practice, demonstrating that predators have these effects on real prey populations has not been easy, and there is still a lot of contention as to the real role of predators on influencing prey populations. Although predation was always thought to be an influential component of insect predator-prey systems (Varley, 1947; Varley & Gradwell, 1968), the impact of higher vertebrate predators on their prey abundance was less clear. From the 1940s to the late 1960s the general consensus was that predators had a relatively small impact on their prey populations. This view was promoted by some influential work by the wildlife ecologists of the day, notably Errington (1946). Errington (1946) suggested that although predators may take large numbers of prey, they do not necessarily reduce the size of the prey's breeding population which is limited by resources. If the overall mortality of the prey population is density-dependent, a reduction in prey numbers by predation may result in a compensatory reduction in density-dependent mortality, so that predation has a small effect on overall abundance. This notion of a doomed surplus was supported by a classic study on red grouse *Lagopus l. scoticus* in Scottish heather moors (Jenkins *et al.*, 1967). These birds form territories in autumn, but the maximum number of territories is limited by habitat suitability, and each year there are a number of non-territorial birds that do not breed. By radio tagging these birds it was possible to determine that non-territorial birds suffered much higher predation rates than territorial birds. Further, if a territorial bird was killed, its territory was rapidly occupied by a previously non-territorial bird. In more recent years, however, there has been mounting evidence suggesting that vertebrate predators have a greater impact on their prey than was traditionally thought.

The strongest evidence comes in the form of predator removal experiments, and these have been supplemented by observations of the response of prey populations to changes

in predator abundance. For example, Marcström *et al.* (1988,1989) showed that spring abundances of mountain hares *Lepus timidus*, capercaillie *Tetra urogallus* and willow grouse *Lagopus lagopus* on Baltic islands were higher following regimes of fox *Vulpes vulpes* and pine marten *Martes martes* control. Another predator removal experiment in southern Britain showed a 2.6-fold difference in the breeding density of grey partridges *Perdix perdix* following a three year regime of predator control (Tapper *et al.*, 1996). Red foxes and feral cats *Felis catus* were removed from a number of sites in the Yathong Nature Reserve in southeast Australia in order to determine their effect on rabbit *Oryctolagus cuniculus* numbers following a drought which had reduced rabbit abundance throughout the reserve (Newsome *et al.*, 1989). After only 14 months, the rabbit populations at predator removal sites were increasing rapidly, whereas the rabbit populations at sites with no predator control remained at low levels for over two years. From an analysis of stomach contents, Pech *et al.* (1992) showed that foxes have a type-3 functional response to rabbit density at these sites, and that the total response of foxes was directly density dependent at low rabbit populations, and inversely density dependent at high rabbit populations. After predators were allowed to return to the predator removal sites, the rabbits there maintained high population densities, and did not decline to the density of the untreated areas. These results suggest that the fox-rabbit system in Yathong Nature Reserve follow the same two-equilibria scheme presented in Figure 1.2. There is some evidence that predators limit rabbit populations in Britain. In England and Wales, Trout & Tittensor (1989) compared indices of rabbit abundance between 203 farmland sites that practised some form of predator removal with 110 sites where no predator control was carried out. The mean indices of rabbit abundance were shown to be significantly higher in predator removal sites. Within predator removal sites, the mean index of rabbit abundance was significantly lower at sites where more predator control effort was exerted. Although this evidence is not conclusive, it suggests that predators are important in limiting rabbit populations in Britain.

In Sweden in the late 1970s and 1980s a national epizootic of sarcoptic mange resulted in a dramatic decrease in the density of foxes. This provided an opportunity for wildlife

biologists to assess the impact of a massive reduction in predator numbers on their prey species which include voles (Cricetidae), hares (*Lepus europaeus* and *L. timidus*) and three species of game bird including capercaillie, black grouse *Tetrao tetrix* and hazel grouse *Bonasa bonasa* (Lindström *et al.*, 1994). The decrease in the abundance of foxes was mirrored by an increase in the abundance of hares and game birds at local, regional and national scales.

Some prey species are vulnerable to predators only in certain age or stage classes. The sensitivity of the growth rate of a population to perturbations in survival or productivity (i.e. due to predation), will vary depending on which age class is being perturbed (Horvitz *et al.*, 1997). Many bird species are most vulnerable to predation at the egg or nestling stage. The way in which nest predation affects the population growth of a bird species will depend on the species' life-history, and how this happens is discussed in the next section.

1.2 The effect of nest predation on bird populations

Nest predation has always been regarded as an important cause of reproductive failure in birds (Ricklefs, 1969), a view which has been supported by numerous studies of nest success. O'Connor (1991), who reviewed 74 studies of nest success, found that the average nest predation rate (± s.d.) was 32.8% ± 22%, and the total nest failure rate was found to be 49.9% ± 20%. A review of 78 different nest success studies (Côté & Sutherland, 1995) showed similar findings: a mean nest predation rate of 38.4% ± 27.1% (s.d.) and a total nest failure rate of 45.5% ± 26.3%. However, high nest predation rates do not necessarily have an effect on the density of breeding populations of birds if there are compensatory decreases in mortality in later stages. For example, McCleery & Perrins (1991) found that a population of great tits *Parus major* maintained a stable population despite heavy predation by weasels *Mustela nivalis* and sparrowhawks *Accipiter nisus* which took up to a third of all young. In an analysis of twenty published

predator removal experiments Côté & Sutherland (1997) found that predator removal significantly increased nest success and the post-breeding population size. However, predator removal had no significant effect on the size of the breeding population in the following year, although this varied considerably between studies.

Tapper *et al.* (1996) found that breeding populations of grey partridges increased significantly after predator removal. Clearly, the effect of nest predation on population growth rate and size will depend on the life history of the bird species, and the patterns of density-dependence determining the size of breeding populations.

Table 1.1 shows some life-history parameters for a selection of ground-nesting bird species from four different orders (Charadriformes, Passeriformes, Galliformes and Anseriformes) obtained from Cramp & Simmons (1983). A measure of the amount of nest predation that can be sustained by a population is given in the final column: this measure is the proportion of eggs that must survive to fledging in order to prevent population decline. Values below this figure will result in population extinction, so high values represent populations that are 'intolerant' of egg and chick predation, and low values represent populations that can sustain relatively high levels of nest predation and still maintain a positive population growth rate. Populations of long-lived birds with relatively high adult survival rates can generally sustain higher egg and chick loss that populations of short-lived birds with lower adult survival rates. The figures shown in Table 1.1 should be treated with caution: the average number of eggs per clutch does not take re-nesting into account and so underestimates total annual egg production, and the maximum ages may be considerably higher than the longevity of most individuals. Further, errors in the measurement of survival rates due to, for example, small sample sizes or samples made during unusual weather conditions, may have a strong effect on the minimum productivity required to prevent population decline.

It is important to note that productivity includes chick survival from hatching to fledging, which may be very different from egg survival from laying to hatching.

Table 1.1 Minimum productivity necessary to maintain ground-nesting bird populations

Species	Group	Clutch size	1st year survival	Adult survival	Maximum age (yrs)	Age at first breeding (yrs)	Minimum productivity to maintain population *a*
Golden Plover *Pluvialis apricaria*	wader	3.85	0.47	0.61	12	1	0.43
Oystercatcher *Haematopus ostralegus*	wader	2.78	0.64	0.85	25+	4	0.28
Lapwing *Vanellus vanellus*	wader	3.74	0.59	0.75	20	1-2	0.25
Skylark *Alauda avensis*	passerine	3.8	0.52	0.66	8	1	0.36
Meadow pipit *Anthus pratensis*	passerine	4.6	0.27	c0.45	8	1	0.89
Red Grouse *Lagopus lagopus*	game	9.8	0.65	0.65	8	1	0.11
Partridge *Perdix perdix*	game	15	0.22	0.44	5	1	0.35
Pheasant *Phasianus colchicus*	game	10	0.19	0.42	7	1	0.61
Mallard *Anas platyrhynchos*	waterfowl	10	0.36	0.45	29	1	0.31
Wigeon *Anas penelope*	waterfowl	9	0.53	0.53	18	1-2	0.20
Canada goose *Branta canadensis*	waterfowl	6	0.78	0.78	23	3	0.16

a Calculated analytically by equating the population growth rate λ to 1 and substituting the life-history parameters for each species into the characteristic polynomial of the population projection matrix, and solving for fledging rate (Caswell, 1997). Maple V mathematical software used for all calculations. Clutch size, survival rates and longevity obtained from Cramp & Simmons (1983).

Some bird populations have been shown to suffer nest predation rates that cannot sustain a steady population. Greenwood *et al.* (1995) showed that the nest success of a variety of duck species nesting in the prairie pothole region of North America was well below that needed to maintain numbers. Similarly, Peach *et al.* (1994) showed that despite high adult survival rates lapwings *Vanellus vanellus* are in decline. They calculated that on average, each pair would have to produce 1.13 fledglings in order to maintain a stable population. Only two of twenty-four estimates of productivity exceeded this threshold (Peach *et al.*, 1994). Although predation is not the only factor associated with poor productivity in lapwings, nest predation has been shown to be high in some cases (Baines, 1990).

Of the 9000 species of birds found around the world, 1029 of these are deemed to be at risk of global extinction (Rands, 1991). Some mammalian predators have expanded their range in recent times and are thought to pose a threat to indigenous fauna. For example, red foxes have been introduced into new areas of California where they were formerly absent or rare, (Lewis *et al.*, 1993) and were introduced into Australia for sport hunting in the 1860s. Foxes are thought to have been responsible for the extinction of a number of small to medium sized mammals and birds in Australia. For example, fox removal studies suggest that foxes are the cause of negative population growth rates in rock-wallabies *Petrogale lateralis* in Western Australia (Kinnear *et al.*, 1988).

As a result of predator range expansions and changes in the availability of nesting habitats, there has been an increased interest in the potential risks that mammalian predators pose to bird populations, particularly in modern landscapes which may favour high densities of predator and low densities of nests (Reynolds & Tapper, 1996).

1.3 Factors promoting the extinction of prey populations by predation

There are two processes by which predators can drive their prey to extinction. The first process is deterministic, and results in the inevitable extinction of the prey population. Deterministic extinction will occur when a predator population maintains a prey consumption rate greater than the prey production rate even when the prey are at a low density. The second process is stochastic: small populations can be strongly influenced by chance events including predation, and can go extinct even if the average productivity of the population is positive (Goodman, 1987; Macdonald *et al.*, 1999). Predation, therefore, may be responsible for the ultimate extinction of a prey population that had initially declined due to other factors such as habitat loss.

Some properties of predators and their prey can contribute to the extinction of prey populations: 1) a prey life-history that promotes slow population growth rate, 2) a prey species with limited anti-predator strategies, 3) an absence or limit to spatial and temporal refugia for prey, 4) a predator species with a wide diet, 5) a predator species with large food requirements or surplus killing behaviour and 6) a predator species that can reach high densities (Atkinson, 1985). The rare California condor *Gymnogyps californianus* has very slow population growth rates, and as a result was almost wiped out by a few 'indifferent' hunters, applying a light 'predation pressure' on the population (Mertz, 1971). This species only survived due to intense conservation efforts, highlighting the vulnerability of slow reproducing species. Perhaps the most dramatic cases of predator mediated extinctions are seen following the introduction of mammalian predators to oceanic islands. Most prey species have evolved strategies for reducing the risk of predation (e.g. Endler, 1991; Caro & Fitzgibbon, 1992), but many island species evolved in the absence of mammalian predators, and lacked adaptations for avoiding or escaping predators. In particular, many island birds have been driven to extinction by introduced mammalian predators such as cats, rats *Rattus* spp. and small mustelids *Mustela* spp. (King, 1984).

The spatial structure of the landscape and the corresponding spatial structure of the prey population can have a number of important effects on extinction risk at different scales (Gilpin, 1987). At a large scale, a fragmented prey population with limited dispersal between fragments (a metapopulation) can persist with high levels of predation, because although predators may drive local populations to extinction, these fragments become recolonised by dispersing prey from other fragments (for a review, see Taylor, 1990). Isolated prey populations, and island prey populations do not receive recruits from elsewhere and are more likely to go extinct (Macdonald *et al.*, 1999). Another effect of fragmenting and reducing the area of suitable habitat is to intensify the spatial overlap of predator and prey activity which can result in inflated predation rates. For example, Potts (1986) found high predation rates on the nests of a declining population of grey partridge *Perdix perdix* in Britain. These birds nest in hedgerows, which present a small area for predators to search leading to high probabilities of nest encounter by mammalian predators (see chapter 6). Habitat fragmentation creates a larger proportion of habitat edges in the environment. Some predators, including red foxes, have been shown to concentrate their activity close to habitat edges (Oehler & Litvaitis, 1996), and numerous studies have shown nest predation rates to be higher in fragmented landscapes (for a review, see Paton, 1994). These results suggest that the large scale alterations of habitats for agriculture and development can have an important influence on predator-prey dynamics.

The red fox can adapt to a wide range of habitat types and has the greatest distribution of any carnivore. As a result of its wide diet, high prey demands and its capacity to kill prey in excess of immediate energetic requirements (surplus killing), the red fox is a prime candidate as a predator capable of driving small or slow growing prey populations to extinction.

1.4 The red fox as a nest predator

The red fox is a classic example of a generalist predator. It has a very wide diet which, in Britain, is usually dominated by small mammals and lagomorphs but also include birds, insects and earthworms (e.g. Harris & Lloyd, 1991). Foxes have been shown to be able to rapidly switch to seasonally abundant food types (Ferrari & Weber, 1995) and will even take large amounts of vegetable matter such as juniper berries when plentiful (Lovari *et al.*, 1994).

In more northern latitudes, the abundance of small rodents such as voles (*Microtus* spp.) and lemmings (*Lemmus* spp.) which are the main prey of foxes in those regions, change dramatically in a cyclical fashion (e.g. Krebs & Myers, 1974, Batzli, 1983). In Fennoscasndia, foxes have been shown to change their diet in response to declines in small mammal abundance (Angelstam *et al.*, 1984). This switch in diet by vole predators during periods of declining vole populations is thought to be the cause of synchronous fluctuations in bird populations and small mammals (e.g. Angelstam *et al.*, 1984; Järvinen, 1990), a notion that has been termed the 'alternative prey hypothesis'. The nest success of a number of bird species has been shown to be negatively correlated with small mammal abundance. Angelstam *et al.* (1984) found that the rate of black grouse nest predation increased from 20% in a year of high vole abundance to over 60% in a year of low vole abundance. In the Tamiyr Peninsula in Siberia, a number of studies have shown that arctic foxes increase their rate of nest predation in years of low or declining lemming abundance (Underhill *et al.*, 1993). The nest success and chick survival of curlew sandpipers *Calidris ferruginea* and the nest success of dark-bellied brent geese *Branta bernicla bernicla* have been shown to be higher during periods of lemming population increase (Summers *et al.*, 1998; Schekkerman *et al.*, 1998). The abundance of arctic foxes, which is linked to the abundance of voles, was shown to be related to the breeding success of brent geese in the following year, which supports the hypothesis that prey switching in arctic foxes is responsible for the relationship between voles and nest success (Summer *et al.*, 1998). The rate of nest predation of a number of wader species, including lapwings and black-tailed godwits *Limosa limosa*, have been negatively

correlated to vole population growth rate in Holland, though in this case, small mustelids are thought to be the predator responsible for this relationship (Beintema & Müskens, 1987). In an analysis of fox scats in Scottish moorland habitats, Leckie *et al.* (1998) found that the occurrence of gamebird remains in scats was unrelated to gamebird abundance. Instead, the frequency occurrence of gamebird remains was related to the abundance of rodents, suggesting that foxes switched to gamebirds in years, or habitats, where rodents were uncommon. These studies suggest that the availability of other prey types is an important factor determining the impact of foxes on the nest success of birds.

It is not possible to detect the remains of birds' eggs in the stomachs or scats of foxes, so fox diets based on stomach contents or scat analysis will underestimate the importance of eggs as a seasonal food source and the importance of foxes as a predator of eggs. However, a number of studies suggest that foxes can have a large impact on the nesting success of birds, particularly waterfowl (e.g. Johnson *et al*, 1989), game birds (e.g. Lindström *et al.*, 1995; Kurki *et al.*, 1997) and colonially nesting seabirds (e.g. Minsky, 1980; Southern *et al.*, 1985). Red foxes have also been known to inflict heavy losses on river tortoise nests in Australia (Thompson, 1983) and green turtle *Chelonia mydas* nests in Turkey (Brown & Macdonald, 1994). A detailed review of the effect of foxes on the nesting success of ground nesting birds will be presented in the next chapter; this section focuses on the physical and behavioural qualities of foxes that may influence their efficiency as a nest predator.

Red foxes are a medium sized carnivore with adults weighing up to 10 kilograms or more. Average weights are less and vary with geographical region. In England, the average weight of a sample of adult male foxes was found to be 6.7 kg, ranging from 5.5 to 8.2 kg (Hattingh, 1956). Females weigh less than dog foxes: a sample of vixens from the same study had an average weight of 5.4 kg. The body size of a predator will have an important influence on what prey can be taken. Foxes are large enough to be able to rob the nests of most ground-nesting bird species and be largely immune from any agonistic behaviour of the incubating birds. Even relatively large birds such as greylag geese *Anser*

anser which can weigh over 4 kg are unable to defend their nests against foxes (Kristiansen, 1998). My own observations have shown that incubating adult greylag and Canada geese *Branta canadensis* may themselves be killed by foxes. There have been unconfirmed reports that foxes have robbed the nests of mute swans *Cygnus olor*, a species weighing up to ten kilograms or more that aggressively defends its nests from any intruders. These reports are not supported by my own observations: a mute swan nesting on a bund across a flooded field never lost any eggs to predators even though fox tracks were regularly seen along the bund close to the swan's nest.

Body size also influences food requirements. Adult foxes require approximately 300-500g of meat per day, and lactating females may require in excess of 1500g of meat per day (Saunders *et al.*, 1993). As a result of such high prey demands particularly during the foxes' breeding season which coincides with that of many birds, foxes have the capacity to eat many clutches of eggs. Even nests with large clutches such as those of ducks, can suffer heavy predation from foxes yet represent a small part of a fox's total diet (Sargeant, 1978). High prey demands during the breeding season are not necessarily restricted to vixens: the dog fox and non-breeding individuals in a fox group can also provision the cubs with food (Baker *et al.*, 1998) as well as hunting to satisfy their own nutritional requirements.

In addition to high prey demands, foxes have a number of behavioural traits that contribute to their importance as an egg predator. Foxes have always been notorious as raiders of chicken coops, and this 'surplus killing' has been observed in colonially nesting seabirds. In a black-headed gull *Larus ridibundus* colony in the north of England, Kruuk (1964) found that up to 230 adult gulls and up to 270 chicks and unquantified numbers of eggs were destroyed in a single night by up to four foxes, with less than 3% of kills being eaten. Red foxes are not the only carnivores that apparently kill prey in excess of immediate requirements. Surplus killing has also been observed in other carnivores, including spotted hyeana *Crocuta crocuta*, leopards *Panthera pardus* and wolves *Canis lupus* (Kruuk, 1972). Surplus killed prey may serve to provide food during periods of

low prey availability, and foxes will sometimes cache food including birds' eggs to be used at a later date (Tinbergen, 1965).

Foxes are able to respond rapidly to seasonal changes in food supply including nesting birds such as eiders *Somateria mollissima* (Wilson, 1990). Foxes in Japan were shown to exploit seasonally super-abundant food resources including spawning salmon and scavenge that were actually beyond their normal territory boundaries, leading to an overlap in territories (Tsukada, 1997). In order to efficiently exploit ephemeral food resources foxes must regularly check all potential feeding sites in their vicinity. The size of fox territories is very variable and range from 0.1 to 20 or more square kilometres (Macdonald, 1981). The efficiency with which foxes can respond to inconspicuous seasonal food resources such as the nests of many waders, ducks and game birds will depend on the rate at which foxes cover their territory and check potential nesting sites. Studies of foxes in urban Bristol in south-western Britain show that foxes usually travel less than 10 kilometres per day, though the mean distance travelled varies between sexes and seasons (Saunders *et al.*, 1993). The territory size of these urban foxes were considerably smaller than the territories of rural foxes and rarely exceeded 50 hectares. Considering the mean daily distances travelled and the small territories of these Bristol foxes, it is feasible that they could check all food patches within their territories in a single night making them particularly efficient at exploiting ephemeral food resources. Comparable data for rural foxes are not available, but considering that the territories of rural foxes are much larger than those of urban foxes (e.g. Ables, 1969; Reynolds & Tapper, 1995) it is unlikely that rural foxes are able to check all patches at the same rate. Prospecting for new food supplies is clearly an important behaviour, and foxes may be particularly efficient at this.

Search behaviour within patches of prey can influence predation rate. Very little is known about how foxes search for birds nests, though unquantified observations by Henry (1977) suggests that foxes use methodical perhaps even systematic search paths to locate scavenge and other small prey types on the ground. Observations by Macdonald

(1980) suggest that foxes are able to concentrate their search effort in areas of high earthworm availability. Efficient search behaviour such as systematic search and site-restricted search can lead to high predation rates, and may be a particularly important component influencing the predation rate of inconspicuous static prey like birds' nests.

Finally, the density of foxes is likely to be restricted by a combination of food limitation and social regulation (Lindström, 1989), and the movement of foxes in spring when most birds in temperate regions are nesting is generally restricted to a territory (e.g. Sargeant, 1972; Reynolds & Tapper, 1995). These limits to the density and movement of foxes during the breeding season of birds suggest that foxes will have a restricted numerical response to high nest densities. Although foxes can be found at high densities in urban areas, greater than 5 family groups per km^2 in Bristol (Harris, 1981), they generally occur at much lower densities in rural areas. Hewson (1986) recorded densities of foxes in Scotland ranging from 0.27 foxes per km^2 in agricultural land to only 0.08 foxes per km^2 in deer forests. These figures support the notion that the numerical response of foxes is indeed limited. However, there is evidence to show that the normal pattern of non-overlapping contiguous territories can shift to overlapping territories around a seasonally abundant food source (Tsukada, 1997). Kruuk (1965) showed that a large black-headed gull colony was exploited by foxes from more than one group which also suggests a temporary breakdown of strict territoriality. This behaviour may have important implications for nest predation rate, particular in areas of high nest density.

In summary, foxes are medium sized carnivores with high prey demands. Foxes are powerful enough to be immune from anti-predator aggression from all but the largest bird species. They have a highly variable diet and have been shown to rapidly exploit seasonal food supplies. Little is known about their patch prospecting and patch exploiting behaviour, but these may be important factors contributing to high nest predation rates. Fox densities are generally low in rural areas, but in circumstances of unusually rich food patches such as colonially nesting sea birds strict territoriality may break down resulting in an increased numerical response to the food supply.

Foxes have traditionally been considered as a pest species in Europe (Reynolds & Tapper, 1996), and in some cases they have been linked with decreased productivity of gamebirds, waterfowl and colonially nesting seabirds. As a result, there has been considerable effort in the control and management of foxes in many parts of their range.

1.5 The management of predation

The deliberate control of predators has been practised for over 2000 years in Europe and has been a part of rural culture that still exists today (Reynolds & Tapper, 1996). Initially, predators were killed in order to protect livestock, to reduce the risk of attacks on humans, and for their fur. Removing predators specifically for the benefit of small game species is a relatively recent practice, and did not start in Britain until the early nineteenth century with the advent of large privately owned sporting estates (Langley & Yalden, 1977). Most recently, predator removal has been carried out by conservationists to promote the continuing survival of rare or endangered species (e.g. Harold, 1994).

Superficially, the objective of predator removal is the same for agriculturists, game managers and conservationists: the reduction of predation on the target species. However, each of these groups have different goals: the agriculturist wants to maximise the harvestable yield of his stock, the game bird manager aims to maximise the autumn post-breeding population for shooting and the conservation manager seeks to maximise the breeding population in the following year to promote maximum reproductive output. These different objectives are met by different predator control regimes. For example, if a prey population experiences density-dependent mortality in winter, a reduction in predation on spring and summer populations may be compensated by an increase in winter mortality. In such an example, predator removal would not meet the objectives of the conservation manager, but might be useful for the game manager. As already mentioned, Côté & Sutherland's (1995) analysis of predator removal experiments found no significant effect on the size of breeding populations in the year following predator

removal, though there was a significant increase in the size of autumn post-breeding populations following predator removal. An important consideration in predator control is the number of predators that need to be removed in order to achieve a particular objective. A conservation manager may tolerate a certain amount of predation of his target species so long as it does not reduce the size of the breeding population in the following year. There may be other criteria determining minimum acceptable levels of predation for the conservation manager. For example, it may be desirable to maximise the number of dispersing animals to augment surrounding populations, in which case, the conservation manager may tolerate less predation. Similarly, targets of minimum acceptable predation levels may be set by agriculturists and game managers that aim to maximise revenue from their stock.

Predator control measures can be expensive both in terms of effort and money. For example, trapping of mammalian predators in order to reduce predation pressure on duck nests in North America cost $24,909 in salaries and although predator removal resulted in higher nesting success (13.5% versus 5.5%), the control resulted in an increase of only 51 nests at the cost of $488 per nest (Sargeant *et al.*, 1995). In order to maximise revenue, the predator population should be reduced to a level at which no further reductions are profitable, or in other words to a level below which the extra costs of control exceed the revenue gained from additional control. This level is termed the economic injury level, and is a common concept in the control of insect pests of crops (e.g. Begon, Harper & Townsend, 1990, pp.553-555). However, the economic injury level is not used as a target for the control of mammalian predators of stock or game for a number of possible reasons: a) variation in the predatory behaviour of individuals makes it difficult to relate predator abundance to predation pressure, b) in sporting estates it may be difficult to measure the revenue from different abundances of game, c) many gamekeepers and other predator managers carry out other management practises making it difficult assess the cost of predator removal in isolation, and d) European rural culture has historically focused on predator eradication (Reynolds & Tapper, 1996).

Predator eradication may be a valid option in some instances. It has already been mentioned that introduced predators can have a large impact on the fauna of oceanic islands, and the complete eradication of these predators is the obvious solution for the conservation of threatened species on such islands. However, even in circumstances where complete predator eradication has a sound economic basis for managers of game and livestock, there are a number of potential problems associated with the loss of a predator species.

Firstly, the local eradication of a predator may contribute to the extinction of the species, which is in conflict with the goal of conservationists. Such persecution by livestock and game managers has created a plethora of predator extinctions world-wide. For example, the grey wolf *Canis lupus* which was the last of the large carnivores in Britain, was hunted to extinction in Britain by the 1700s (Yalden, 1999). Several endangered canids continue to be threatened by predator management today, including the relict populations of grey wolves in Mexico, Spain and Italy, and the African wild dog *Lycaon pictus* (Ginsberg & Macdonald, 1990). Predator control has the potential to drive common species to extinction. The ubiquitous red fox was very scarce in East Anglia as a result of intense control by gamekeepers during the nineteenth century (Tapper, 1992). Perhaps the reason why foxes in Britain did not decline to the same extent as other medium sized predators such as wild cats *Felis silvestris* and pine martens *Martes martes* was their status as a quarry species, which lead to a number of management practices that actually promoted stable fox populations (Langley & Yalden, 1977; Yalden, 1999).

The second potential problem associated with the loss of a predator is an unwanted increase in a prey species. For example, in the early twentieth century, mule deer *Odocoileus hemionus* populations on the Kaibab Plateau in Arizona expanded rapidly following a cessation in hunting and the removal of a guild of predators. The large numbers of deer caused considerable damage to their habitat throughout their range, and by the mid 1920s the herd decreased dramatically in numbers largely due to starvation (Leopold *et al.*, 1947; Lack, 1954). Studies in Australia suggest that predators are

capable of regulating potential pest species such as house mice *Mus domesticus* and rabbits under certain conditions (Newsome *et al.*, 1989; Sinclair *et al.*, 1989; Pech *et al.*, 1992). Clearly, removing the predators of these prey species could result in higher densities of a potentially more problematic and economically damaging pest.

A third potential problem arising from the removal of predators may be a reduction in intra-guild predation on smaller predators leading to mesopredator release, an increase in the abundance of smaller, and possibly more problematic predators (Polis, Myers & Holt, 1989; Litvaitis & Villafuerte, 1996). Intra-guild predation has been reported by many ecologists, and examples include red foxes preying on arctic foxes *Alopex lagopus* (Schamel & Tracy, 1986; Hersteinsson & Macdonald, 1992), pine martens (Lindström *et al.*, 1995), and weasels (Latham, 1952). Red foxes themselves have been the prey of larger carnivores, including coyotes *Canis latrans* (Sargeant & Allen, 1989) and lynx *Felis lynx* (Stephenson *et al*, 1991). Not only have coyotes been shown to prey upon red foxes, they also exclude them from their territories (Sargeant *et al.*, 1987; Harrison *et al.*, 1989). This can have important consequences for prey species. In the prairie pothole region of the northern United States, Sovada *et al.* (1995) found that an average of 32% of duck nests survived to hatching in coyote dominated areas compared to only 17% in red fox dominated areas. This difference was caused by different nest predation rates by foxes between areas: only 4% of predated nests were attributed to foxes in coyote areas whereas 27% of predated nests could be attributed to foxes in areas where foxes were the principal canid.

The ethics of predator removal have been hotly debated, particularly in western culture, for the last few decades. Although the culture and ethics of predator control do not necessarily contribute to a pragmatic approach to predator management, the culture and debate surrounding predator removal has stimulated funding for wildlife research as well as motivating the actions of agriculturists, game managers and ranchers, and so deserves some attention here. Two issues are prominent in the debate: 1) whether or not the management objectives justify predator removal and 2) whether or not animals suffer

from control operations, and if so whether or not the amount of animal suffering is an important issue. There are several ultimate motives for killing predators: 1) self preservation, 2) to promote the survival of a rare species 3) to promote the survival of a game species and 4) for food. Most people would probably consider improved human safety as a valid objective justifying the removal of dangerous predators. The removal of predators for conservation poses a more complicated ethical problem: does the rarity of a prey species truly justify predator removal? Perhaps the most emotive ethical problem lies in the removal of predators to increase the abundance of game so that they may be shot in greater numbers. The second issue considers animal suffering. One view is that any predator removal is justifiable so long as the amount of suffering experienced by the animal during removal operations is kept below an acceptable level. In reality, measuring suffering objectively is very difficult, and defining what is an 'acceptable level' of suffering is equally difficult to define or quantify. Despite the difficulties associated with measuring and defining animal suffering, the ethics of animal suffering are reflected in law. The methods that can be used to kill animals are restricted by law in some countries: in Britain, for example, it is now illegal to use leg-hold or 'gin' traps and snares must be free-running and be checked at least once every 24 hours. In an influential study on the effects of hunting with hounds on stags *Cervus elaphus*, Bateson & Bradshaw (1997) showed that stags hunted in this way built up very high levels of cortisol, a common indicator of intense stress in mammals. As a result of this study, the hunting of stags with hounds was banned on land owned by the National Trust in the UK.

There are clearly a number of practical, biological and ethical problems associated with predator removal, and as a result, it may preferable to adopt an approach that minimises lethal predator control. An approach that matches the 'integrated pest management' philosophy for the control of large scale agricultural pests may be appropriate for the control of mammalian predators as well. In integrated pest management minimum acceptable levels of a pest are identified, and the objective of control is to maintain the pest below these levels. A wide variety of control techniques are considered in the integrated pest management of agricultural pests, with an emphasis on promoting natural

mortality from natural enemies and weather. An integrated approach for the control of mammalian predators may include strategies that reduce predation on the game species by altering its profitability relative to other prey types. Foraging theory shows that predators may exclude relatively unprofitable foraging patches from their 'diet', if on average, they yield less energy per 'handling' time than the average rate of energy gain from its territory as a whole (e.g. Stephens & Krebs, 1986). It may be possible to alter the relative profitabilities of different foraging areas using a variety of habitat management techniques to promote higher densities of other prey species. In many areas, the breeding seasons of birds and their egg predators coincide. Some important egg predators, including red foxes, provision their own young at a central place. The location of the central place with respect to food patches can theoretically influence a predators' choice of foraging patch (e.g. Stephens & Krebs, 1986), and therefore, the management of den sites is a potential management tool for reducing predation on a target species (Larivière & Messier, 1998b). Other potential management strategies for reducing the effect of predators on nest success include: 1) the promotion of natural enemies of the pest species (e.g. Sovada *et al.*, 1995); 2) the use of exclosures (e.g. Minsky, 1980); 3) conditioned taste aversion (Conover, 1990); and 4) supplementary feeding (Durdin, 1993). Some of these techniques have shown to be ineffective in certain cases. For example, in a Florida beach habitat, the use of nonlethal oestrogen laced eggs to induce conditioned taste aversion in racoons did not reduce the rate of green turtle egg predation by racoons (Ratnaswamy *et al.*, 1997). Although predator exclosures have been shown to be effective in many cases (e.g. Beauchamp *et al.*, 1996), electric fences were shown to be ineffective in preventing foxes accessing tern colonies in Norfolk (Musgrave, 1993). In some cases, lethal predator control may remain the best option to achieve management objectives.

1.6 Thesis structure

This thesis is divided into one review chapter, four data chapters and a general discussion.

In chapter 2, I present a comprehensive review of the effect of foxes on the nest success of three orders of ground-nesting birds. The importance of the red fox as a nest predator of some species of ground-nesting bird is far from clear. One of these species, the lapwing, is a grassland wader of conservation interest due to recent population declines in Britain and other parts of its range.

In chapter 3, I test the hypothesis that carrion crows are a more important lapwing nest predator than foxes at a mixed farming site in England. In an environment free of foxes, carrion crows have been shown to generate a characteristic negatively density-dependent pattern of nest predation, brought about by improved communal nest defence by denser groups of nesting adult lapwings (Berg *et al.*, 1992).

Several authors have described fox searching behaviour (Henry, 1977; Macdonald, 1981; Sonerud, 1988). However, there is no published data available for the search behaviour of foxes in wader nesting habitats. Lapwing nests are small and relatively dispersed, which probably makes them a relatively unprofitable prey type. However, it has been hypothesised that such birds may suffer heavy nest loss due to incidental predation - the random or fortuitous encounter of a prey item that does not elicit any change in search behaviour (Vickery *et al.*, 1991). In chapter 4, I describe the nocturnal search behaviour of foxes in lapwing nesting colonies, and present evidence for site-restricted search in response to cues from breeding lapwings. In addition, I show that foxes are capable of carrying out systematic searches in linear habitats, a behaviour that may have important consequences for prey in modern agricultural landscapes.

The way in which a predator responds to the density of its prey can be crucial in its effect on prey populations. In chapter 5, I test the hypothesis that search effort by foxes in wetland nesting habitats is dependant on the density of breeding ground-nesting birds.

Most ground-nesting bird species can only nest in particular habitats. In many modern landscapes such patches are reduced in area and highly fragmented. Some predators,

including the red fox, are thought to be able to exploit this by restricting their search to particular habitat fragments. In chapter 6, I use a computer model that mimics fox search behaviour to determine the sensitivity of nest predation rate to changes in the area of nesting habitat. The movement parameters used in the model are obtained from direct observations of foxes in nesting habitats.

In the final chapter the significance of these findings for the management of nest predation by foxes are discussed, along with avenues of future work.

2. A review of the effect of foxes on the nest success of ground-nesting birds

Summary

1. Evidence for the effect of foxes on waterfowl and game-birds comes from predator exclosure and removal experiments. This evidence has been supplemented by large scale studies comparing nest predation in areas of high and low fox activity. Foxes can be an important predator of the nests of these groups of birds, but their relative importance may vary with region and habitat. More information is needed to determine the influence of local landscape characteristics, habitat types and predator assemblages on nest predation by foxes.

2. Colonially nesting sea-birds can suffer high nest loss to foxes if they have access to nesting sites. Predator exclosures have been effective in preventing nest loss to foxes in several cases.

3. From 98 measures of nest predation in waders obtained from the literature, there were only 11 reliable measures of nest predation by foxes from eight different studies. Mayfield estimates of nest predation by foxes ranged from 0 to 58.8%, with a mean of 20.4 ± 22.34% (s.d.). Seven of these nine studies are of beach-nesting waders.

4. The only reliable estimate of fox predation on ground-nesting passerine clutches comes from two studies carried out in southern Spain, which present nest predation rates of 34% or more (Suárez & Manrique, 1992; Yanes & Suárez, 1996). No estimates of the contribution of foxes to nest predation rate were available in the other nineteen studies reviewed.

2.1 Introduction

Nest predation is one of the most important factors influencing the reproductive success of birds, and can vary considerably between species and location (Ricklefs, 1969; O'Connor, 1991, Côté & Sutherland, 1995). It was traditionally thought that ground-nesting bird species suffer higher nest predation than off-ground nesting species (Ricklefs, 1969, Collias & Collias, 1984), but there is increasing evidence to weaken the validity of this view. Martin (1993) measured the nest success of passerines nesting in different vegetation layers, and found that in forests, ground nests experienced a lower rate of nest predation (30.6%) than nests in the shrub layer (45.5%) and the tree canopy (35.4%). However, in shrub/grassland habitats ground nests suffered significantly higher predation rates (48.8%) than nests in shrubs (40.0%). In a comparison of 98 measures of nest predation in cavity nests, burrow nests, open and closed cup off-ground nests and ground nests, Côté & Sutherland (1995) found that predation rates of ground nests were not significantly different from other nest types, except cavity nests. They also found that predation rate on ground nests in shrub/grassland habitats did not differ significantly from shrub nests. In an artificial nest experiment carried out in southcentral Sweden, Soderstrom *et al.* (1998) found that nest predation rates were significantly higher in shrub nests than ground nests. In this study, the principal predators of shrub nests were corvids, whilst mammals were the most important predators of ground nests. These results are counter intuitive because one would expect ground nests to be more accessible to a wider variety of predator species.

Some species of ground-nesting bird, especially ducks and game-birds, are hunted for sport, and are of economic importance in rural areas of Europe and North America. Other species of ground-nesting birds, particularly waders such as lapwings, are becoming rare in certain parts of their range, and are of interest to conservationists. Nest predation can be a critical factor in determining the abundance and growth of bird populations. As a result, there is a considerable interest in determining the relative importance of different

nest predators of ground-nesting birds, so that rare or economically important ground-nesting birds can be managed more effectively.

Most species of nest predator are patchily distributed around the world, being restricted to particular zoogeographical regions. As a result, the relative contribution of different species of nest predator to nest loss will also vary around the world. In northern temperate regions, the most significant nest predators are rodents, carnivores, and predatory birds, particularly corvids and larids (for a review, Côté & Sutherland, 1995). In warmer temperate areas, snakes can also inflict heavy losses on the eggs of smaller birds (e.g. Best, 1978; Wray *et al.*, 1982). Even insects have been known to influence the breeding success of birds: the southern fire ant *Solenopsis xyloni* has been shown to reduce the breeding success of the endangered California least tern *Sterna antillarum browni* (Hooper *et al.*, 1998). In the tropics, important nest predators can also include primates such as the long-tailed macaque *Macaca fascicularis* (Safford, 1997), monitor lizards and snakes such as the brown tree snake *Boiga irregularis* (Conry, 1988). The red fox is a potentially important ground nest predator with a particularly bad reputation amongst game bird managers (Tapper, 1992). Red foxes have the widest distribution of any carnivore. They are found throughout Europe and the majority of temperate Asia and Japan. Red foxes are also common in most parts of North America being found as far south as central Texas. They were introduced into Australia by European settler in 1868 and have now spread over much of the continent.

There are three main reasons why different ground-nesting bird species would be expected to suffer different rates of predation by foxes. Firstly, the clutches of ground-nesting birds range in size considerably from around 14 g for an average clutch of skylark *Alauda arvensis* eggs to around 900 g for an average clutch of greylag goose eggs (Cramp & Simmons, 1983). As a result, they represent quite different food rewards to foxes and may be expected to elicit different amounts of foraging effort. Secondly, ground-nesting birds have evolved a large number of strategies to reduce the risk of nest predation, which are likely to vary in their effectiveness against foxes. For example, some ground nesting

species, particularly seabirds and waterfowl, often place their nests on islands that are inaccessible to foxes and other mammalian predators. Thirdly, ground-nesting birds nest in a variety of habitats which, on a large scale, may support different numbers of foxes (e.g. Kurki *et al.*, 1998), or on a smaller scale, may be used to varying extents by foxes (Jones & Theberge, 1982; Oehler & Litvaitis, 1996). The contribution of red foxes to the nest predation rates of some groups of ground-nesting birds has been well studied. These groups include waterfowl (Anseriformes), game birds (Galliformes) and colonially nesting sea-birds, especially gulls (Laridae) and terns (Sternidae), and the principal evidence for the role of foxes as a nest predator of these groups are presented in Sections 2.3.1, 2.3.2 and 2.3.3. The effect of foxes on the nest success of other groups of ground-nesting birds, namely waders (Charadriformes) and Passerines, is less well known. In order to evaluate the impact of foxes on nest predation of waders and ground-nesting passerines, a comprehensive review of nest predation in these groups is presented in Section 2.3.4 and Section 2.3.5 along with the evidence implicating foxes as the nest predator.

2.2 Identifying nest predators

There are a number of practical problems associated with the identification of nest predators. Given that the nests of most birds species are incubated for two to three weeks, identifying nest predators from direct observation would require very long surveillance periods to ensure that predation events were actually seen. In addition, many predators are active at night, and even with modern night viewing equipment, predators may be difficult to detect under certain conditions (see Section 4.2.2). The presence of observers in the vicinity of the nest site could influence the probability of nest predation either by altering the behaviour of predators or the incubating birds (Major, 1990). The identification of nest predators by direct observation of predation events is a labour intensive technique and rarely used.

Some bird species nest on soft substrates allowing predators to be identified by their tracks. For example, snowy plovers *Charadrius alexandrius* and piping plovers *Charadrius melodus* frequently nest on sandy substrates, and it has been possible to identify the predators of the nests of these species by animal tracks around the nest (Page *et al.*, 1983; Patterson *et al.*, 1991). The relative importance of predators of nests found in different habitats could differ considerably from predators of nests found on open sandy or muddy substrates. Therefore, it would be wrong to assume that the predators identified from tracks are of equal importance to the success of nests in habitats such as grassland where clear tracks are not left by predators.

Some ecologists have attempted to identify predators from the remains of predated nests. For example, in a study of the nesting success of field sparrows *Spizella pusilla* in Illinois, Best (1970) associated intact empty nests surrounded by undisturbed vegetation with snakes. Predated nests that had been moved and were surrounded by flattened vegetation were associated with medium sized mammalian predators such as red foxes and grey foxes *Urocyon cinereoargentus*. In this case, direct observations suggested that predators were correctly identified by nest remains. Some researchers have identified predators of waterfowl nests from the appearance and disposition of nest remains (e.g. Rearden, 1951). However, the validity of using the remains of waterfowl nests to identify nest predators is doubtful. Larivière & Messier (1997) observed 34 predation events on natural and simulated waterfowl nests by striped skunks *Mephitis mephitis*. They concluded that the variable patterns and temporal dynamics in the appearance of nests predated by skunks preclude researchers from identifying predators solely on the basis of nest remains. Green *et al.* (1987) suggested that the predators of waders' eggs can be identified by the nature of tooth marks in the shell remains. They showed that the distance between pairs of toothmarks on shells may give some indication of which mammalian predator was responsible. Further, eggshell remains with toothmarks were associated with crushed edges suggesting that this is also a feature of mammalian predators. The main problem with this technique is that in many cases there are no shell fragments available for analysis. This problem may vary between species: for example,

Green *et al.* (1987) showed that egg fragments were less likely to be found around lapwing nests than redshank or snipe nests. Willebrand & Marcström (1988) adopted a novel approach for the identification of egg predators of black grouse *Tetrao tetrix*. They introduced radio-tagged eggs into black grouse nests. Each radio-tagged egg consisted of a similarly coloured chickens' egg containing a radio transmitter embedded in paraffin. The radio transmitter allowed the researchers to locate the egg, and the paraffin provided an ideal medium for the identification of tooth or beak marks. This technique has been used by Brittas *et al.* (1992) to identify the predators of pheasant *Phasianus colchicus* nests. Incubating pheasant hens were occasionally killed by predators, and the remains of the hen and the presence of scats also helped Brittas *et al.* (1992) to identify nest predators. These methods may not be suitable for other ground nesting species, such as passerines and waders that have relatively small clutches or smaller eggs. Radio-tagged eggs in the clutches of these species would alter the appearance of the nest and potentially influence the behaviour of predators or the incubating bird.

A number of researchers have used remote cameras to identify nest predators. Some workers have used remote cameras to identify predators at specially designed dummy nests, with manual or electronic cameras triggered by movement of nest contents (Major, 1991; Danielson *et al.*, 1996) or by infra-red systems (Savidge & Seibert, 1988). Remote cameras have also been used to identify the predators of real nests including those of New Holland honey-eaters *Phylidonyris novaehollandiae* (Major & Gowing, 1994). The main benefit in using remote cameras to identify nest predators is that there is no ambiguity in the results. Photographs also allow individual predators within a species to be recognised, which allows the researcher to assess the relative importance of individual predators or specific age classes of predator. However, there are a number of drawbacks in the use of remote cameras to identify nest predators. The triggering system may in some cases interfere with the nest, which may influence the probability of nest predation. Non-invasive triggers such as infra-red light beams may be preferable. Cameras with an automatic film forwarding mechanism are preferable in order to record repeated predation

events or to reset the camera after being triggered by non-predators (e.g. the incubating bird). In order to record nocturnal predation events the camera needs to be equipped with a flash, which may influence predator behaviour. All these requirements will tend to make remote cameras an expansive option for identifying predators. Danielson *et al.* (1996) present a relatively inexpensive automatic camera system for wildlife research, but even at US $110 per piece, any study that aims to assess the relative impact of different predators in a given season will need a good sized sample of nests (>20) making this method very expensive. One study of the breeding biology of Wilson's plovers *Charadrius wilsonia cinnamonius* in Venezuela used a time-lapse infra-red video system to record the behaviour of plovers at the nest (Thibault & MacNeil, 1995). Although the area covered by nocturnal video surveillance is not likely to be greater than a few hectares at most (Stewart *et al.*, 1997), such a system may be particularly useful in a) recording nest predation behaviour of nocturnal predators and b) identifying the predators of a large sample of nests in colonially nesting bird species. Nocturnal video-surveillance equipment and associated power supplies are very expensive, bulky, difficult to maintain and run the risk of being stolen in the field (Stewart *et al.*, 1997).

There are clearly many difficulties associated with the direct identification of nest predators. As a result, many researchers have used indirect evidence to assess the relative importance of different nest predators. For example, comparing the predation rate of nests inside and outside a selective predator exclosure will give an indication of the importance of excluded predators. Similarly, comparing the predation rate of nests in areas that differ in the abundance of a particular predator species can also provide indirect evidence of the importance of that species as a nest predator. In the following section I present evidence for the impact of foxes on the nesting success of waterfowl, game-birds and colonially nesting sea birds.

2.3 A review of the effect of foxes on the nest success of ground-nesting birds

2.3.1 Anatidae (waterfowl)

The two most familiar and abundant tribes of waterfowl are the Anserini which include swans and geese, and the Anatini, which include the dabbling ducks. Both groups contain economically important game species in North America and Europe, including Britain (e.g. Tapper, 1992; Norton & Thomas, 1994). Some waterfowl, such as the lesser white-fronted goose *Anser erythropus*, have become rare (Madsen, 1991), and are the target of conservation efforts (Vonessen, 1991; Vickeray *et al.*, 1994). The need for the management of waterfowl for game production and conservation has promoted a large number of studies on nest success and predation.

The prairie pothole region in North America covers over 777 000 km^2 of southcentral Canada and the northcentral United States, and is of particular importance for the production of North American dabbling ducks (Anatini). Although it contains only 10% of the American breeding range, this area produces around 50% of North American ducks (Smith *et al.*, 1964). The abundance of several waterfowl species in the region declined in the 1980s (U.S. Fish & Wildlife Service, 1986). The productivity of mallards and other species have been shown to be well below the level needed for self-sustaining populations (Cowardin *et al.*, 1985; Greenwood *et al.*, 1987; Greenwood *et al.*, 1995; Klett *et al.*, 1988), and more recently, the nest success of five duck species including mallard, gadwall *Anas strepera*, blue-winged teal *A. discors*, northern shoveller *A. clypaeta* and northern pintail *A. acuta* have been shown to decrease significantly over time from 1935 to the early 1990s (Beauchamp *et al.*, 1996). The main cause of nest loss has been shown to be predation (Klett *et al.*, 1988), and it has been hypothesised that predation rates have increased over time as a result agricultural intensification of the prairie pothole region and the subsequent reduction and fragmentation of nesting cover (Pasitchniak-Arts & Messier, 1995; Larivière & Messier, 1998). There are a wide range of potential waterfowl nest predators in the prairie pothole region which include red

foxes, striped skunks *Mephitis maphitis*, coyotes, racoons *Procyon lotor*, American badgers *Taxidea taxus* and rodents. There are also a number of avian predators of duck eggs in the region, principally American crows *Corvus branchyrhncos* and gulls (*Larus* spp.).

The main type of evidence implicating mammals as the main duck egg predators comes from comparisons of the success of duck nests exposed to mammalian predators, with those not exposed to mammalian predators. Beauchamp, Nudds & Clark (1996) compared 21 measures of duck nest success where mammalian predators were removed by trapping, shooting or poisoning, or were excluded by fences or open water, with 37 nest success studies conducted in sites where predators were not removed or excluded. They showed that the nest success on islands or in mammalian predator exclosures was significantly greater than the nest success in unmanaged or predator removal sites. Interestingly, they noted a significant decline in duck nest success over time from 1935 to 1995 that was paralleled in sites with and without mammalian predators, suggesting that mammalian predators are not responsible for the temporal pattern. In a five year study of the breeding success of mallards and gadwalls nesting on a small island free of mammalian predators, Duebbert *et al.* (1983) reported a nest success of 85% for both duck species despite the presence of ring-billed gulls *Larus delawarensis* and California gulls *Larus californicus*, both of which were known to rob eggs from duck nests. Lagrange *et al.* (1995), who carried out a 12-year study of the nest success of mallards and blue-winged teal in northcentral Iowa, found that the nest success of both species was significantly higher inside electric fence predator exclosures than outside. The difference in nest success was considerable: outside the exclosure, the nesting success of both species of duck was only 14%, whilst inside the exclosures, the nest success was 39% for mallard and 30% for blue-winged teal. The electric fence did not exclude stoats *Mustela erminea* and other small mammalian predators or avian predators. Although the predators that still had access to duck nests robbed many nests, the overall nest success of mallard and blue-winged teal within the exclosures was easily high enough to maintain a steady population (Klett *et al.*, 1988).

In a large-scale study of duck nest success, Cowardin *et al.* (1998) compared the nest success of dabbling ducks in three widely separated 25 hectare predator exclosures with the nest success of ducks outside exclosures. The nest success of ducks in the exclosures averaged 72% over the five year study and was substantially higher then the nesting success of ducks in similar habitats outside the exclosures. These exclosure experiments indicate that medium to large-sized mammalian predators are the most important predators of duck eggs in the prairie pothole region and surrounding areas.

There is some evidence to suggest that the red fox is the most important predator of duck eggs in the prairie pothole region. Between 1983 and 1985, Johnson *et al.* (1988) related the predation rates of over 3000 duck nests distributed across sixteen study sites in the Canadian prairie pothole region, to indices of activity of eight egg-eating predators. Indices of carnivore activity were derived from the abundance of carnivore tracks measured from thorough searches of each 16 × 1.6 km study area. They found that nest predation rates in the early part of the breeding season were positively related to indices of fox, American badger and crow activity, and later in the breeding season, predation rates were positively related to indices of fox and skunk activity. In addition, Johnson *et al.* (1988) showed that indices of fox abundance are negatively correlated with coyote abundance; this is not surprising in the light of what is now known about the relationship between these two species. Since coyotes prey upon foxes and displace them from their centres of activity (Sargeant, Allen & Hastings, 1987; Harrison, Bisonette, & Sherburne, 1989), comparing the nest success of ducks in areas of high and low coyote activity allows wildlife biologists to assess the relative impact of these two canids on nest predation. In North Dakota and South Dakota, Sovada *et al.* (1995) compared the nest success of ducks in 17 separate areas dominated by coyotes (determined by track surveys) with the nest success of ducks in 13 areas where the red fox was the principal canid. In fox areas, duck nest success averaged only 17% compared with 32% in coyote dominated areas. In six areas where both canids were common, duck nest success averaged 25%. The habitat composition and the variety of other predators was similar across all sites. Predated nests with characteristics of fox predation accounted for 4% of losses in coyote

areas and 27% of all losses in fox areas, showing that predation by foxes did indeed account for the differences in nest success. Similar results were found by Ball *et al.* (1995) in north-central Montana. In this study, variation in dabbling duck nest success across seven grassland habitat blocks appeared to be associated with the presence of foxes versus coyotes, as well as the size of the habitat block.

The evidence of these studies suggest that the red fox is an important predator of duck nests that can reduce nesting success to levels below that required to maintain a steady population. They also suggest that the management of coyotes may be an effective method of reducing the impact of foxes on duck nest success. The red fox is not the only important nest predator in the prairie pothole region. As already mentioned, the indices of skunk activity have been positively related to duck nest predation rate in the later half of the nesting season from mid to late June in the Canadian prairie pothole region (Johnson *et al.*, 1988). Striped skunks have also been identified as the principal predator of artificial waterfowl nests in at least two studies (Patischniak-Arts & Messier, 1995; Larivière & Messier, 1998) accounting for 44% and 67% of artificial nest losses in each study. Although skunks are somewhat smaller than foxes, usually weighing between 2 to 5 kg, they are also generalist predators with potentially high prey demands during the waterfowl nesting season, when they provision their young at a den (Larivière & Messier, 1998b). Given the many similarities in the ecology of striped skunks and red foxes, it is not surprising that they are both shown to be important predators of duck nests. Although most of the evidence implicating foxes as the most important duck nest predator comes from the prairie pothole region, it is possible that foxes are important predators of duck nests in other parts of their range.

There are a number of possible reasons why duck nests are so susceptible to predation by medium sized carnivores. Firstly, duck nests probably represent a particularly profitable prey type to medium sized carnivores. The nests of dabbling ducks are quite large, usually containing between 6 to 12 eggs. For example, a typical clutch of mallard eggs weighs in the region of 500 g (Cramp & Simmons, 1983), providing enough food to

satisfy the daily energy requirements of an adult fox (Saunders *et al.*, 1993). Secondly, the anti-predator strategy of dabbling ducks, which rely on either crypticity and sitting tight on the nest or highly vocal distraction displays (Cramp & Simmon, 1983; Jacobsen & Ugelvik, 1992) may be relatively ineffective against generalist predators that search the ground methodically for a variety of small prey types (Henry, 1977). Thirdly, duck nests may present particularly strong olfactory cues to mammalian predators, allowing them to locate them efficiently even if nests are well concealed in vegetation. Although the relative nest detection efficiencies of different egg predators are not know, skunks have been shown to increase their olfactory detection efficiency with increasing experience of particular food types (Nams, 1997).

The larger waterfowl from the tribe Anserini, which includes the swans and geese, have also been shown to suffer heavy losses to large and medium sized mammalian predators. Arctic foxes in particular have an important effect on the breeding success of geese. In a study of breeding goose populations in southeast Svalbard (Madsen *et al.*, 1992), arctic foxes prevented brent geese, barnacle geese *Branta leucopsis* and pink-footed geese *Anser brachrhynchos* from breeding on many of the small islands where they usually nest. It is probable that arctic foxes become stranded on some of these islands during the break-up of sea ice in spring. At one island, a fox had apparently arrived after nest initiation and destroyed 45 brent goose and barnacle goose nests. Studies of goose nesting success in Siberia also indicate that arctic foxes are amongst the most important predators of goose nests (Syroechkovskiy *et al.*, 1991; Spaans *et al.*, 1993; Spaans *et al.*, 1998; Summers *et al.*, 1998), though avian predators have also been shown to be important (Spaans *et al.*, 1998). Red foxes are also predators of goose eggs, though less information is available. In a study of the nest success of greylag geese in Danish reedbeds, Kristiansen (1998) showed that mammalian predators, which included red foxes, American mink *Mustela vison* and polecats *M. putorius*, robbed 15% of all nests in the study. At one site in the Lower Derwent Valley in the north of England, I monitored seventeen canada goose nests in 1997 (see Chapter 3). Of these only two were known to be predated, and at least fifty goslings were hatched from 82 eggs. In addition, only one

out of twenty greylag goose nests that were monitored in the same area showed any evidence of having been predated. Foxes were thought to visit the site nightly, yet nest predation was very low even though the dikes on which the geese nested were accessible to foxes, though only by a convoluted system of dikes. Trip-wire activated photo-traps on the dikes showed that foxes never walked along the dikes where the geese nested. At the same site in 1998 heavy flooding forced the geese to nest in unusual sites. After the floods receded, many nests were left exposed, and these suffered heavy predation by foxes. On one 100 metre stretch of dike the nests of 8 greylag geese and 8 canada geese were all predated by foxes. At least two incubating canada geese were known to have been predated by foxes. One of these had been nesting on a small island in a pond, and incubated the nest for at least two weeks before it was killed. The water level of the pond had dropped dramatically during this period, and fox tracks showed that the fox had crossed to the island at a point where the water was no deeper than 10 cm, and had circumvented the island up to the point of the goose nest. Clearly, the availability of good nest sites is of prime importance to the nest success of geese.

To summarise, foxes can be very important predators of waterfowl nests. The evidence that implicates the red fox as the main nest predator also suggest possible management techniques to reduce predation by foxes: 1) create islands in lakes of sufficient depth and size to exclude foxes, 2) create predator exclosures with electric fencing, and 3), improve the quality (especially cover) and area of nesting habitat (Crabtree *et al.*, 1989; Larivière & Messier, 1998; McKinnon & Duncan, 1999). Most of the evidence implicating foxes as the major predator of duck nests comes from the prairie pothole region of North America. Although the studies of duck nest predation come from widely distributed sites in and around the prairie pothole region, they may not be representative of nest predation elsewhere in the world.

2.3.2 Galliformes (Game Birds)

Many species of Galliform are extensively shot for sport in North America and Europe, and populations are often managed to provide a surplus of birds for the guns in the autumn shooting season (Leopold, 1933). Game bird shoots are widespread in Britain and can be an important part of rural economies (Hudson, 1992). Predator control has traditionally been an important part of game management (Leopold, 1933; Reynolds & Tapper, 1996), and red foxes are considered as the most important game bird predators (Darrow, 1947; Tapper, 1991). The control of predation on game bird populations may also be important from the perspective of conservation. Within the range of the red fox, there are over twenty species of galliform that are classified as vulnerable, endangered or critically endangered by the International Union for the Conservation of Nature (IUCN). The majority of these species are found in China and northern India, and little is known about the effect of foxes on these species. The malleefowl *Leiopa ocellata,* found in Australia is classified as vulnerable by the IUCN. The drastic reduction in population size and range of this species has been attributed to habitat loss and chick predation by red foxes and feral cats along with native raptors (IUCN, 1999).

A number of species in Britain have undergone considerable reductions in population size, including the grey partridge *Perdix perdix* (Marchant *et al.*, 1990; Potts & Aebischer, 1995), red grouse *Lagopus lagopus scoticus* (Barnes, 1987; Hudson, 1992) and black grouse *Tetrao tetrix* (Hancock *et al.*, 1999). All have been listed as species of conservation concern (Batten *et al.*, 1991). Although changes in farming practice and habitat management are known to be important factors influencing these population declines (Potts, 1986; Hudson, 1992; Lovegrove *et al.*, 1995; Baines, 1996) predation is thought to exacerbate the problem, particularly in the grey partridge (Tapper *et al.*, 1996). However, predation may not be a problem for all British game birds: Baines (1996) showed that the presence of gamekeepers on moorlands did not influence black grouse breeding success depot a threefold reduction in avian egg predators in keepered areas. As

a result of the game and conservation status of many Galliformes, and the reputation of the red fox as vermin on shooting estates, a considerable amount of research has been carried out to determine the effect of foxes on game bird populations.

Some of the best evidence for the impact of foxes on game bird nest success and survival comes from Scandinavia. In a large scale study in Finland using 100 × 100 km squares as sample units, Kurki *et al.* (1997) found that the breeding success of black grouse and capercaillie *Tetrao urogallus*, measured as the proportion of hens with broods in late spring per square, was negatively correlated with the relative densities of two generalist predators, red foxes and pine martens *Martes martes*. The breeding success of these birds showed no spatial relationship with stoat abundance, a more specialised predator. In the late 1970s to the late 1980s, the red fox population of Sweden was greatly reduced by an epizootic of sarcoptic mange (Lindström, 1992). The relative abundances of a number of game bird species in central Sweden, including black grouse, capercaillie and hazel grouse *Bonasa bonasa* were all shown to increase during the height of the mange event when fox populations were at their lowest, and to decrease as the fox population recovered in the early 1990s (Lindström *et al.*, 1994). More evidence comes in the form of predator removal experiments: Marcström *et al.* (1988) removed foxes and pine martens from one of two islands in the northern Baltic and reversed the treatment after four years of control. During predator removal, 77% of the hens of both species had chicks compared to only 59% when foxes and pine martens were present. Broods were smaller in the presence of predators: mean August brood size in the absence of predators was 5.52 compared with 3.29 in the presence of predators. An increase in adult black grouse and capercaillie numbers of 56 to 80% was noted after two years of predator control. Other egg predators, including small mustelids and corvids were not removed in this study, showing that the difference in breeding success and survival was due to foxes and pine martens. These results suggest that in Scandinavia, foxes are an important predator of game birds and their eggs.

In Britain, foxes are considered to be one of the main predators of incubating grey partridges (Tapper *et al.*, 1982; Potts, 1986), and second only to raptors as predators of red grouse (Moss *et al.*, 1990; Hudson, 1992; Thirgood & Redpath, 1997). In an experiment to determine the effect of predators on grey partridge productivity and abundance, Tapper *et al.* (1996) removed a number of predator species, including foxes, from one of a pair of study sites in the south of England. One site was subjected to predator removal for three years, whilst in the other site the predator community was undisturbed. These treatments were then reversed between sites and run for a further three years in order to remove any site specific effects on partridge productivity. Predator control significantly increased productivity and resulted in higher autumn and breeding stocks. Since a number of predator species were removed, it is not possible to determine the relative importance of foxes as nest predators from this study.

The advent of miniature radio-transmitters has allowed ecologists to follow the fate of marked birds (Marcström *et al.*, 1989). A number of studies have used radio tags to monitor the survival of marked birds during spring, when the hens are incubating (Table 2.1). The recovery of dead birds often allows the researcher to ascertain the cause of death. There are a number of signs around a kill that indicate predation by a fox, and these include scats, footprints, feathers sheared by carnassial teeth, half buried prey remains (typical of fox caches) or location close to an earth. The figures in Table 2.1 suggest that foxes are important predators of game birds, especially incubating hens during the breeding season. However, there is some evidence to suggest that radio tags influence hen survival, so the results should be treated with some caution (Reynolds *et al.*, 1991).

In addition to killing incubating hens, there is evidence that foxes prey on the eggs and chicks of game birds. Leif (1994) found that medium sized carnivores, including red foxes, skunks and racoons, predated 44% of ring-necked pheasant nests in his South Dakota study site. In Iowa, Riley *et al.* (1998) implanted tiny radio transmitters into 332 pheasant chicks from 117 broods, in order to measure their survival rates. The mortality

rate of these chicks up to 28 days of age was approximately 60%. The largest cause of mortality (> 85%) was predation by stoats, red foxes and American mink (in order of importance). In a sample of 345 pheasant nests in England, foxes were the most important predator, accounting for 30% of predated nests, but contributing only 7% to the total nest mortality rate (Cramp & Simmons, 1980). In a study of 7521 partridge nests in Britain between 1911 and 1934, 1,956 (22%) were destroyed before hatching (Middleton, 1936). Red foxes were reported to be responsible for 34% of these losses, making them by far the most important nest predator of grey partridges in this period.

Table 2.1 Predation rates on game birds during the nesting season. M indicates males, F indicates hens. All examples are wild birds.

Species	Location	*n*	% Predation by foxes	% Total predation	Source
Pheasant	South Dakota	(M + F) 44	?	45.4	Leif (1994)
Pheasant	England & Ireland	(F) 69	27.0	?	Hill & Robertson (1988)
Pheasant	Sweden	(F) 307	20.2	38.4	Brittas *et al.* (1992)
Pheasant	Sweden	(M) 172	9.0	26.0	Grahn (1993)
		(F) 188	8.0	25.0	
Pheasant	Iowa	(F) 215	< 12.7	16.7	Schmitz & Clark (1999)
Red Grouse	Scotland	(F) 121	≥16.5	38.0	Moss *et al.* (1990)
Spruce Grouse	Maine	(F) 19	?	37.0	Whitcomb *et al.* (1996)
Grey Partridge	England	(F) 52	38.5	57.7	Reynolds *et al.* (1991)

These results suggest that foxes are an important predator of game birds, their eggs and chicks. There are a number of possible hypotheses to explain why foxes are apparently such important predators of many species of galliforms: 1) Incubating game birds and their nests are particularly profitable for foxes, 2) the anti-predator responses of game

birds are ineffectual against foxes and 3) a shortage of other prey types in modern landscapes increases predation pressure. Similar to waterfowl nests, game bird nests and incubating hens are relatively large, providing a profitable reward for foxes. Table 2.2 below shows the weights of the clutches and incubating hens of various species, giving an indication of the profitability of these potential prey items to red foxes.

Table 2.2 Hen weight, egg weight and clutch size for a selection of European game birds. Data from Cramp & Simmons (1980).

Species	Hen Weight (g)	Mean Egg Weight (g)	Clutch Size
Pheasant	720 - 1000	33	8 - 15
Grey Partridge	364 - 416	14	9 - 18
Red Grouse	550 - 660	25	6 - 9
Black Grouse	856 - 1120	35	6 - 11
Capercaillie	1500 - 1950	48	7 - 11

For many species of galliform, the incubating hen and her clutch will provide enough food to easily satisfy the daily energy requirements of a fox (Saunders *et al.*, 1993).

The nests of many game birds including red grouse, pheasant, grey partridge and black grouse are well hidden in vegetation and very difficult to detect by sight. In addition, the nests of most species are solitary and well spaced out, a defence against predators that adopt site restricted search tactics (Tinbergen *et al.*, 1967; Taylor, 1976). During the breeding season, female red grouse stop producing caecal faeces and their scent emissions drop considerably: the maximum detection distance for trained pointing dogs decreases from around 50m in winter to less than half a metre during the incubation period (Hudson *et al.*, 1992). It is possible that the fragmentation and reduction in area of nesting habitat in agricultural landscapes reduce the efficiency of these cryptic anti-predator strategies (Larivière & Messier, 1998). For example, partridge hens frequently nest in the vegetation alongside hedgerows, and Potts (1986) suggested that high nest predation rates occurred because predators capable of concentrating their search to the small area of

remaining hedgerows would experience high nest encounter rates. This concept is explored theoretically in Chapter 6. As already noted, the incubating hens of a number of game bird species are particularly susceptible to predation by foxes. Some game birds, including ring-necked pheasants and grey partridges, stay on the nest at the approach of a predator, relying on their camouflage to avoid attracting the predator. A different anti-predator strategy, particularly common amongst waders such, is to quit the nest whilst the predator is still far away (Byrkjedal, 1987). Waders lose considerably fewer incubating birds to predators than game birds (see Section 2.3.4), suggesting that a 'sit-tight' strategy is less effective against mammalian predators. Brooding grouse hens sometimes perform distraction displays that include injury feigning and a heavy laborious flight, after being flushed by a predator (Cramp & Simmons, 1980). An observation of two consecutive encounters between a red fox and grouse (black grouse and capercaillie) in Norway, showed that not only did their distraction displays fail to draw the attention of the fox, it appeared to elicit a site restricted search behaviour at the point where the bird was initially flushed, resulting in the predation of grouse chicks (Sonerud, 1988). All this evidence suggests that the anti-predator behaviour of game birds is of limited use against red foxes.

Studies in northern latitudes where the abundance of microtine rodents, a main prey of foxes, fluctuate dramatically in a cyclical pattern, show that during peaks in rodent abundance, the predation rate on game birds decreases (Angelstam *et al.*, 1984; Järvinen, 1990). In more southern latitudes, where there are no marked cycles in microtine abundance, it is possible that spatial variation in main prey abundance (lagomorphs and rodents) influences the predation rate of foxes on game birds. For example, in a study in Scotland, Leckie *et al.* (1998) found that the frequency of occurrence of game birds in fox scats was negatively related to rodent abundance, and they concluded that foxes switched to game birds in years or habitats when rodents were uncommon.

In summary, foxes are clearly important predators of game birds and their eggs in many parts of their range. Game birds may be particularly susceptible to fox predation because

a) they are a profitable prey item for foxes, b) their habit of sitting tight on the nest puts incubating hens at considerable risk from predation, c) distraction displays are ineffectual against foxes, d) low main prey abundance in agricultural habitats causes foxes to switch to birds and e) modern agricultural landscapes provide relatively little nesting cover that is easily searched by predators.

2.3.3 Colonially nesting birds

A number of different bird species habitually nest in colonies, notably the gulls and terns (Laridae) and seabirds of the order Procellariiformes, which include petrels, albatrosses and shearwaters. Other species, such as eider ducks *Somateria mollissima*, occasionally nest in dense colonies. The nesting densities of many of these species is very high, with large numbers of birds nesting within a few metres on one another, making these nesting colonies a very conspicuous and rewarding target for predators. Predators such as foxes capable of surplus killing would be expected to inflict heavy losses on nests and chicks if given access to colonies.

There is strong evidence to suggest that foxes can have a severe impact on the reproductive success of colonially nesting birds. Rimmer & Deblinger (1992) used a non-electric wire mesh fence to exclude terrestrial predators from a least tern *Sterna antillarum* colony on a barrier beach in Massachusetts. The hatching rate of nests within the exclosure was 73% ($n = 227$), considerably higher than the hatching success outside the fence, which was only 12% ($n = 227$). The majority of nest failures outside the fence were due to medium sized mammalian predators including red foxes and racoons. At another colony of nesting least terns on a sand spit in Massachusetts, a red fox was known to have regularly foraged in the colony over a period of 7 days, reducing the number of nests from 139 to 45 (Minsky, 1980). At the end of the 7 day period an electric fence was erected, and the absence of fox tracks inside the exclosure showed that the fence was working. The number of nests within the exclosure increased to 85, suggesting that the

fox was responsible for earlier losses. Red foxes have been shown to inflict heavy losses on Caspian tern *Sterna caspia* colonies on the shores of Lake Ontario, whilst terns nesting on off-shore rafts inaccessible to foxes, raised an average of 1.9 chicks per pair to fledging (Lampman *et al.*, 1996). In Florida, Gore & Kinnison (1991) compared the breeding success of least terns nesting on flat gravel-covered roofs with that of ground nesting colonies. Ground colonies suffered heavy nest predation and an average of only 10.4% of eggs from ground nests hatched. The nest predators identified from tracks in the sand in the colony (frequently leading from one empty nest to the next), were red foxes, racoons and domestic cats. There was no evidence of mammalian predators on roof nesting colonies, perhaps not surprising considering the different nesting substrate. However, the nesting success of roof colonies was significantly higher at 29.4%. On Scolt Head Island on the north Norfolk coast, foxes have been shown to have caused the complete breeding failure of a large colony of sandwich terns *Sterna sandvicensis* for three years running (Musgrave, 1993). Foxes have also been identified as the most serious predator at a sandwich tern colony in Scotland (Forster, 1975). Terns are not the only colonially nesting birds to suffer heavy predation from foxes.

In one breeding season on Shaiak Island off the Alaskan coast, red foxes were reported to have destroyed every nest in common eider and glaucous-winged gull *Larus glaucescens* colonies (Petersen, 1982). In a black-headed gull colony in the north of England, Kruuk (1964) found that up to 230 adult gulls and up to 270 chicks and unquantified numbers of eggs were destroyed in a single night by up to four foxes, with less than 3% of kills being eaten. I have also recorded evidence for surplus-killing of black-headed gull chicks in a colony in North Yorkshire: extensive fox tracks in the gull colony and bite marks in chick kills identified foxes as the cause of death of at least twenty-five chicks in two nights. None of these chicks showed any signs of having been eaten. Out of 92 nests monitored, only 18 showed signs of having been robbed. The larger herring gull *Larus argentatus* has also been known to suffer heavy chick predation by foxes. On South Manitou Island in Lake Michigan, red foxes removed chicks from at least 45% of marked nests, causing the attendant adults to desert and cease incubation of remaining unhatched

eggs (Shugart & Scharf, 1977). Foxes were identified as the predator from tracks in the colony and canine puncture marks in the chick carcasses. Southern *et al.* (1985) showed that the continued presence of red foxes on South Manitou Island over a nine-year period regularly caused the complete breeding failure of herring gulls and ring-billed gulls *Larus delawarensis*, and resulted in a dramatic decline in colony size in both species.

There is no doubt that foxes can catastrophically reduce the breeding success of colonially nesting bird species if they have access to nesting colonies. Some species of tern may abort breeding attempts completely if foxes regularly disturb breeding colonies (Patterson, 1977), making them particularly vulnerable to foxes. Many tern colonies are targeted for conservation because they represent internationally important breeding populations (e.g. sandwich terns at Scolt Head Island) or because the population is small or in decline. For example, California least terns are classified as endangered throughout their range by the United States Department of the Interior and protection from predators is high on the agenda for conservation measures (Butchko & Small, 1992). The black tern *Chlidonias niger* population of North America has been shown to be declining at an average rate of 3.1% per year between 1966 and 1996 (Peterjohn & Sauer, 1997), and the breeding population of the roseate tern *Sterna dougallii* in northwest Europe has declined from 3812 pairs in 1968 to only 561 pairs in 1987, a reduction of 85% (Cabot, 1996). The fairy tern *Sterna nereis* which nests on beaches and coastal islands of southern Australia, New Caledonia and New Zealand is classified as vulnerable by the IUCN. Predation by red foxes may be a problem for beach nesting colonies of this globally rare species in Australia.

2.3.4 Charadriformes (Waders)

A number of wader species are rare or experiencing population declines, and as a result there has been considerable interest in determining the factors affecting the breeding success of these species. At least four species of wader that breed within the range of the red fox are classified as vulnerable by the IUCN, including piping plovers *Charadrius melodus* and mountain plovers *Charadrius montanus* of North America, hooded plovers *Charadrius rubricollis* of southern Australia and the bristle-thighed curlew *Numenius tahitiensis* of western Alaska (Collar *et al.*, 1994). There are also a number of waders species whose populations are declining regionally, such as the lapwing in western Europe (Tucker *et al.*, 1994) and the snowy plover population of the west coast of the United States (Page *et al.*, 1991).

The evidence presented in the previous sections show that foxes can be one of the most important predators influencing the nest success of waterfowl, game birds and colonially nesting waterbirds. However, waders might be expected to suffer lower nest predation rates from foxes than the ground-nesting species considered in the previous section for several reasons. Firstly, the clutches of most wader eggs are considerably smaller and lighter than those of waterfowl and most game birds, and therefore provide a less profitable meal for foxes. Curlews *Numenius arquata* are one of the largest species of wader, with a typical clutch of 4 eggs weighing around 310g. The clutch weight of most waders is much less than this, ranging from 27g for small species like the snowy plover *Charadrius alexandrius* to 100g in larger species such as lapwings. As a result, foxes may be expected to invest less effort in searching for them. Secondly, the nests of most wader species are solitary or dispersed, a strategy that can reduce nest predation by mammals and other predators that use area-restricted search patterns (Tinbergen *et al.*, 1967; Taylor, 1976, Hogstad, 1995). Thirdly, many waders are vigilant whilst incubating their eggs, selecting sites that allow them to detect the approach of a predator whilst it is still far away from the nest (Byrkjedal, 1987). Many waders (e.g. lapwings)

will quit the nest whilst the predator is some distance away. This behavior presumably makes it very difficult for ground predators to locate the nest.

A review of 63 studies of the breeding biology of waders within the global range of the red fox yielded 98 separate estimates of nest predation rates for 34 different species. These data are summarised in Table 2.3. Some studies presented data from more than one site. Only pooled data are presented in Table 2.3, but for the purpose of statistics I have considered measures of nest predation to be independent if the sites are greater than four kilometres apart, a distance large enough to ensure that each area experiences different predators. The mean percentage of nests robbed by all predator species is 39.12 ± 22.29% (s.d.), ranging from 0% to 97.4%. Measuring nest predation as the ratio of the number of predated nests to the total number of nests may underestimate nest predation rates, especially if many nests in the sample are found late in the incubation period. This is because predated nests are usually harder to locate than incubated nests, this making them under-represented in the sample. Mayfield (1961,1975) overcame this bias by measuring nest predation as a daily probability, which is calculated by dividing the number of nests lost to predators by the total number of nest days. The expected survival rate is calculated by raising the daily probability of surviving predation to the power *j*, where *j* equals the number of days elapsed between the first egg laid and the last chick hatched. The expected predation rate is obtained by subtracting this figure from 1. From the fifty-one studies that provided Mayfield estimates for predation rate, the mean percentage predated is 49.24 ± 26.20%, ranging from 0 to 99.9%.

Table 2.3 Nest predation rates of waders. Predator codes: 1= red fox, 2 = striped skunk, 3 = racoon, 4 = American badger, 5 = Eurasian badger, 6 = Arctic fox, 7 = small mustelids, 8 = rodents, 9 = corvids and/or gulls, 10 = snakes, 11 = other canids. † Figures in brackets represent predation rates by all medium sized carnivores including red foxes, grey foxes, arctic foxes, skunks, racoons and badgers. Predation rates marked * were calculated using the Mayfield method (Mayfield, 1975), otherwise they were calculated as the ratio of predated nests to total nests. Latin names are presented alphabetically in Table 2.6.

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Piping plover	North Dakota	Beach	150	?	58.5*	1-4, 7-11	Prindiville Gaines & Ryan (1988)
Piping plover	Southern Manitoba	Beach	72	(27.8)	27.8	1-4,7-11	Haig & Oring (1988)
Piping plover	Massach-usetts	Beach	76	55.3, (55.3)	55.3	1-3, 7-11	MacIvor *et al.* (1990)
Piping plover	Virginia	Beach	122	29.2*, (41.5*)	51.8*	1-3	Patterson *et al.* (1991)
Piping plover	Massach-usetts	Beach	24	33.3, (45.8)	75.0	1-3,8-11	Rimmer & Deblinger (1990)
Piping plover	Saskat-chewan	Beach	69	?	18.8	1-4,7-10	Espie *at al.* (1996)
Mountain plover	Colorado	Prairie	101	?	13.9	2-4,7-11	Graul (1975)
Mountain plover	Colorado	Prairie	20	?	25.0	2-4,7-11	McCaffery *et al.* (1984)
Mountain plover	Colorado	Prairie	102	?	21.6	2-4,7-11	Knopf & Rupert (1996)
Snowy plover	South France	Beach	700	?	c.90	1,5,7-10	Lessells (1984)
Snowy plover	Oklahoma	Beach	123	?	5.6*, 13.0	2-4,7-11	Koenen *et al.* (1996)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Snowy plover	Utah	Beach	414	17.1, 31.0*, (19.1), (33.8*)	39.1, 57.4*	1-3,9	Paton (1995)
Ringed plover	UK	Beach	70	12.8, 34.5*	78.6, 93.2*	1,9	Pienkowski (1984)
Ringed plover	Greenland	Tundra	?	?	32.2*	6,9	Pienkowski (1984)
Eurasian dotterel	Norway	Tundra	51	?	30.2, 47.4*	1,6,7,9.	Byrkjedal (1987)
Semi-palmated plover	Northern Manitoba	Tundra	61	?	27.9	1,6,7,9.	Armstrong & Nol (1993)
Wilson's plover	Texas	Beach	58	(≥10.3), (≥21.2*)	36.2, 56.9*	2,3,9-11	Bergstrom (1988)
Killdeer	Ontario	Beach	17	0, (23.5), (38.0*)	70.6, 76.7*	1-3,7-11	Nol & Brooks (1982)
Killdeer	California	Beach	45	?	57.8, 84.6*	1-3,7-11	Ohlendorf *et al.* (1989)
Golden plover	Norway	Tundra	51	?	52.9, 78.2*	1,6,7,9	Byrkjedal (1987)
Golden plover	Scotland	Moor	76	18.4	81.6	1,7,9	Parr (1993)
Long-billed curlew	Idaho	Meadow	119	(28.6), (46.6*)	35.3, 54.1*	1-4,7-10	Redmond & Jenni (1986)
Long-billed curlew	Oregon	Meadow	101	(8.4), (16.7*)	14.7, 27.5*	1-4,7-10	Pampush & Anthony (1993)
Curlew	Sweden	Meadow	92	?	43.5, 63.7*	1,5,7-10	Berg (1992)
Curlew	Sweden	Arable	15	?	13.3, 22.1*	1,5,7-10	Berg (1992)
Curlew	Ireland	Meadow	154	?	74.0, 91.5*	1,5,7-9	Grant *et al.* (1999)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Curlew	Ireland	Meadow	143	?	58.7, 81.5*	7- 9	Grant *et al.* (1999)
Whimbrel	Northern Manitoba	Tundra	25	?	36.0	1,6-9	Jehl (1971)
Whimbrel	Northern Manitoba	Tundra	65	?	18.5, 29.4*	1,6-9	Skeel (1983)
Whimbrel	Shetland	Moor	113	0 (0)	12.7	9	Grant (1991)
Stilt sandpiper	Northern Manitoba	Tundra	43	?	11.6	1,6,8,9	Jehl (1971)
Spotted sandpiper	Minnesota	Island	317	0 (0)	29.3	7,8,9	Oring *et al.* (1983)
Least sandpiper	Northern Manitoba	Tundra	56		10.7	1,6,8,9	Jehl (1971)
Pectoral sandpiper	Alaska	Tundra	39	0, (?)	97.4, 99.9*	6,9	Estelle *et al.* (1996)
Buff-breasted sandpiper	Alaska	Tundra	18	0, (?)	61.1	6,9	Pruett-Jones (1988)
Common sandpiper	England	Moor	88	?	11.4	1,7,9	Holland *et al.* (1982)
Common sandpiper	England	Moor	30	0, (0)	10.3	1,7,9	Cuthbertson *et al.* (1952)
Dunlin	Alaska	Tundra	42	?	19.0	6,7,9	Holmes (1966)
Black-necked stilt	California	Beach	464	?	44.4, 69.0*	1-3,7-11	Ohlendorf *et al.* (1989)
American avocet	California	Beach	169	?	47.2, 67.7*	1-3,7-11	Ohlendorf *et al.* (1989)
Avocet	Holland	Meadow	?	?	25.3*	1,7-9	Beintema & Müskens (1987)
Temminck's stint	Norway	Tundra	65	?	8.0, 10.4*	1,6,7,9	Breiehagen (1989)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Temminck's stint	Finland	Meadow	208	?	41.8	1,7,8,9	Hilden (1978)
Temminck's stint	Finland	Meadow	117	?	43.6	1,7,8,9	Koivula & Rönkä (1998)
Oystercatcher	Holland	Meadow	?	?	42.7*	1,7-9	Beintema & Müskens (1987)
Black-tailed godwit	Holland	Meadow	?	?	39.2*	1,7-9	Beintema & Müskens (1987)
Black-tailed godwit	Poland	Meadow	80	?	47.5	1,7-9	Dyrcz *et al.* (1981)
Ruff	Holland	Meadow	?	?	2.3*	1,7-9	Beintema & Müskens (1987)
Ruff	Poland	Meadow	29	?	69.0	1,7-9	Dyrcz *et al.* (1981)
Redshank	Holland	Meadow	?	?	29.7*	1,7-9	Beintema & Müskens (1987)
Redshank	England	Pasture	361	?	3.0	1,7-9	Nethersole-Thompson & Nethersole-Thompson (1986)
Greenshank	Scotland	Moor	106	3.9	14.2	1,7-9	Nethersole-Thompson & Nethersole-Thompson (1979)
Snipe	England	Meadow	207	≥ 0.5	≤ 33.3	1,7-9	Mason & Macdonald (1976)
Snipe	England	Meadow	256	?	29.3	1,7-9	Green (1988)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Snipe	Holland	Meadow	?	?	10.8*	1,7-9	Beintema & Müskens (1987)
Snipe	Poland	Meadow	61	?	31.2	1,7-10	Dyrcz *et al.* (1981)
Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Lapwing	Holland	Meadow	?	?	47.9*	1,7-9	Beintema & Müskens (1987)
Lapwing	Poland	Meadow	32	?	28.1	1,7-10	Dyrcz *et al.* (1981)
Lapwing	Scotland	Moor	135	?	57.8, 71.0*	1,7,9	Galbraith (1988)
Lapwing	Scotland	Arable	93	?	44.1, 58.3*	1,7,9	Galbraith (1988)
Lapwing	England	Pasture: un-improved	347	?	46.7	1,7,9	Baines (1990)
Lapwing	England	Pature: improved	109	?	75.6	1,7,9	Baines (1990)
Lapwing	England	Meadow: un-improved	96	?	52.7	1,7,9	Baines (1990)
Lapwing	England	Meadow: improved	78	?	51.8	1,7,9	Baines (1990)
Lapwing	England	Arable	88	?	24.6	1,7,9	Baines (1990)
Lapwing	Orkney	Moor	75	0 (0)	42.7	9	Cuthbert (1983)
Lapwing	England	Pasture	48	?	60.4, 60.6*	1,7,9	G.Hibberd, Holme NWT, unpublished data

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Lapwing	England	Pasture	17	?	5.9, 6*	1,7,9	Exminster Marshes RSPB, unpublished data
Lapwing	England	Pasture	35	?	37.1, 39.5*	1,7,9	Nene Washes RSPB, unpublished data
Lapwing	Sweden	Pasture and arable	870	?	12.9, 14.7*	1,5,7-9	Berg (1992)
Lapwing	Scotland	Pasture	37	?	33.8, 37.0*	1,5,7,9	Redfern (1982)
Red-necked phalarope	Northern Manitoba	Tundra	245	?	45.3	1,6-9,11	Reymolds (1987)
Wilson's phalarope	North Dakota	Island	23	?	95.6	1-4,7-10	Kagarise (1979)
Wilson's phalarope	Southern Sakatch-ewan	Meadow	386	?	56.3	1-4,7-10	Colwell & Oring (1988)

From the 98 independent estimates of nest success, there were only 11 reliable measures of nest predation by foxes, which came from eight different studies. Seven of these studies are of beach-nesting waders including piping plovers (Haig & Oring, 1988; MacIvor *et al.*, 1990; Rimmer & Deblinger, 1990; Patterson *et al.*, 1991), snowy plovers (Paton, 1995; Koenen *et al*, 1996) and ringed plovers (Pienkowski, 1984). The remaining two studies are moorland nesting waders: greenshank (Nerthersole-Thompson & Nerthersole-Thompson, 1979) and golden plover (Parr, 1993). The mean proportion of these wader nests lost to foxes is 13.6 ± 12.5%. Only nine Mayfield estimates of fox predation were available from the data, and these ranged from 0 to 58.8% (mean 20.4 ± 22.34%). A number of other medium-sized carnivores were recorded as having robbed

wader nests, including skunks, racoons, arctic foxes, American badgers and other fox species. There are eighteen studies in which nest loss to medium-sized carnivores, including red foxes, is distinguished from nest loss to other predators. The mean proportion of nests robbed by these predators is 23.28 ± 22.34 %. The corresponding Mayfield estimate for nest predation by medium sized generalist predators is 27.74 ± 21.73 % (n = 14), an estimate obtained mostly from beach nesting species.

Measurements of nest predation by foxes and other mammalian predators are biased to beach nesting waders. This is not surprising, because sandy substrates allow predators to be distinguished by footprints. The effect of foxes and other mammalian predators may be different in other habitats, but it was not possible to test this with the data available. Total nest predation rates from all predators in temperate areas (i.e. arctic studies excluded) were not significantly different on beach habitats compared with other habitat types, and did not appear to be influenced by location (Table 2.4). The latter result is perhaps surprising considering the greater diversity of medium sized (1 - 10kg) carnivores in North America than the United Kingdom and Europe. However, it was not possible to control for the interaction between habitat and location because of the limited number of studies of nest success of beach nesting waders in continental Europe.

Table 2.4 ANOVA for the effect of location (North America, continental Europe, UK) and habitat (beach, other habitats) on total nest predation rate (arcsine transformed).

Source	*d.f.*	SS	MS	*F*	*P*
Location	2	0.03227	0.01613	0.25	0.780
Habitat	1	0.02587	0.02587	0.40	0.530
Error	64	4.14627	0.06479		
Total	67				

Additional evidence for the effect of foxes and other medium-sized mammalian carnivores on the nesting success of waders comes from predator exclosure experiments, which are also biased towards beach nesting waders. Rimmer & Deblinger (1990) used wire mesh fences to exclude mammalian predators from 26 piping plover nests on a Massachusetts beach. Only two (8%) of the nests in exclosures were predated, compared to 18 out of 24 unexclosed nests. Red foxes were shown to be the most important nest predator at this site, accounting for eight of the predated nests. Red foxes are considered as a serious threat to the breeding success of snowy plovers in Utah, and in a four year study, Paton (1995) showed that the average probability of losing snowy plover nests to foxes during the incubation period was 31%. Red foxes are also thought to be a major problem for snowy plovers nesting in California (Point Reyes Bird Observatory, unpublished data). A preliminary nest exclosure study in the Monterey Bay area of coastal California showed that nests in wire mesh exclosures suffered significantly lower predation rates than nests outside exclosures (Dixon, unpublished report from the Resources Agency of California). In a two-year study at an Oklahoma salt flat coyotes, the most frequent mammalian predator, were shown to predate 37% ($n = 94$) of all charadriform nests, including those of snowy plovers (Grover & Knopf, 1982). In a later study at the same site, electric fences were used to exclude predators from snowy plover nests (Koenen *et al.*, 1996). The proportion of plover nests lost to predators in the exclosures was 5.8% ($n = 52$), and was not significantly different from the proportion of snowy plover nests predated outside the exclosures, which was only 10.6% ($n = 123$). The lack of effect of the predator exclosure is surprising, since tracks around predated nests in Grover & Kopf's (1982) study indicated that coyotes were the most important predator. Factors that could cloud the effect of the exclosure include poor exclosure design, and increased predation rates by non-enclosed predators such as gulls and corvids. A predator exclosure experiment with killdeer *Charadrius vociferus* nests illustrates the importance of exclosure design: the predation rate of 12 exclosed and 17 unexclosed nests by mammals was not significantly different, largely because both racoons and small mustelids were able to reach nests in exclosures (Nol & Brooks, 1982). In Alaska, small wire mesh cages were used to exclude both avian and mammalian predators from pectoral

sandpiper *Calidris malanotos* nests (Estelle *et al.*, 1996). Arctic foxes were believed to be the most important nest predator in this case, but the design of the exclosure did not allow the researchers to test this. Arctic foxes attempted to dig under nine of the thirteen nest exclosures, but they may have been attracted to the exclosures themselves, so this does not necessarily reflect the nest visitation rate of foxes outside the exclosures.

A number of workers studying the breeding biology of mountain plovers in Colorado have shown that swift foxes *Vulpes velox* are predators of both the eggs (Graul, 1975) and chicks (Miller & Knopf, 1993; Knopf & Rupert, 1996) of mountain plovers. However, since the sample sizes are small in these studies, and the effect of radio-transmitters on chick vulnerability has not been assessed, it is not possible to draw any conclusions about the importance of swift foxes as a predator of mountain plover eggs and chicks.

In a recent study of the breeding biology of curlews in Northern Ireland, predators were shown to inflict heavy losses to eggs (Grant *et al.*, 1999). At one area in county Antrim, the average nest predation rate over a 32 day laying and incubation period was 90.2%, whilst the nest predation rate in Lough Erne, which was largely free of foxes, was also very high, averaging 79.6% over two years. The authors concluded that the majority of nest predation in the Antrim area was probably caused by foxes, but the evidence is far from conclusive. Wax eggs which would allow the identification of egg predators from toothmarks or bill marks were shown to increase the predation rates of nests in the Antrim area, and so give potentially biased information. Out of 11 intensively monitored nests in the Antrim area, eight were lost overnight indicating predation by nocturnal mammalian predators. Only three out of twenty predated nests with identifiable remains indicated predation by foxes. This study illustrates the difficulty in identifying nest predators of grassland waders.

Despite being relatively small prey items, wader nests appear to be frequently robbed by mammalian predators, including large ones such as coyotes. Red foxes have been identified as an important predator of waders nesting on sand or shingle, such as piping

plovers and snowy plovers. Mayfield estimates of nest predation by foxes for these species range from 0 to 58.8%, with a mean of 20.4 ± 22.34%. The sample size for this estimate is small ($n = 9$), and more measures are needed to provide a more general measure of the impact of foxes on wader nest success. In addition, grassland and tundra nesting waders are under-represented in this sample, and may differ in their susceptibility to foxes.

Sovada *et al.* (1995) measured the predation rate of 193 duck nests in thirteen different sites known to host relatively high densities of foxes. The Mayfield estimate for nest predation rate by foxes at these sites was 36.7%, somewhat higher than the mean nest predation rate of wader nests. However, in order to make a useful statistical comparison of the effect of foxes on the nest success of different bird species, more independent Mayfield estimates of nest predation by foxes are needed from a wider range of geographical locations and habitats.

2.3.5 Passeriformes

A number of passerine birds nest on or near the ground in easy reach of non-arboreal predators such as red foxes. The largest families of ground-nesting passerines include the Alaudidae (larks), the Motacillidae (pipits and wagtails) and the Embezeridae (New World sparrows). Some of these species are of conservation concern in areas within the range of the red fox. For example, in Europe a number of lark species including the skylark *Alauda arvensis*, the thekla lark *Galerida theklae* and the lesser short-toed lark *Calandrella rufescens*, are rare or declining in number, and enjoy special conservation status (Tucker *et al.*, 1994b). The rate of nest predation has been found to be high in a number of ground-nesting passerines (e.g. Suárez & Manrique, 1992), and this has generated an increased interest in identifying the predators responsible in order to improve management strategies for increasing productivity.

The nests of ground-nesting passerines are very small compared with the nests of other ground-nesting species. The small size of passerine nests, and the relative ease at which they can be concealed in vegetation, would suggest that they are relatively inconspicuous to a predator the size of a fox. The clutch weight of most lark and pipit species is considerably less than 20g, making a meal that would contribute less than 3% to an adult foxes' daily food requirement (Saunders *et al.*, 1993). As a result, foxes would not be expected to actively search for the nests of passerines.

A review of 21 studies of the breeding biology of 25 species of ground-nesting passerines yielded 35 measures of nest predation (Table 2.5). The percentage of nests lost to predators varied from 0 to 76.2%, with a mean of 35.6 ± 17.61% (s.d.). Mayfield estimates of nest predation were available in 25 cases, and averaged 50.06 ± 17.31%. This value is not significantly different from the Mayfield estimate for nest predation in waders (using arcsine transformed data, $t = 0.14$, $d.f. = 69$, n.s.). Only one study provided a direct estimate of the contribution of foxes to nest predation rate. In a study of arid shrubsteppe nesting birds in southern Spain, Suárez & Manrique (1992) showed that foxes robbed 18.9% of black-eared wheatear *Oenanthe hispanica* nests. The total probability of black-eared wheatear nest predation by foxes throughout the incubation and nestling stages was shown to be 34.0%. Red foxes are the most important predator of other shrubsteppe birds in the same Spanish study site, including the thekla and lesser short-toed larks (Yanes & Suárez, 1996). These larks were shown to experience very high nest predation rates averaging 87% ($n = 235$) across sites and years. Predators were identified from tracks at 38 predated nests: 86% of these were identified as foxes or feral dogs. It is possible that these canids were over-represented in this sample, because being the heaviest nest predators in the area, they were the most likely to leave tracks. However, daily survival rates of lark nests at different sites were negatively correlated with independent measures or fox and feral dog abundance, whereas no such correlation was found for other egg predators such as snakes, hedgehogs and shrikes.

Table 2.5 Nest predation rates of ground-nesting passerines. Predator codes: 1= red fox, 2 = striped skunk, 3 = racoon, 4 = American badger, 5 = Eurasian badger, 6 = Arctic fox, 7 = small mustelids, 8 = rodents, 9 = corvids and/or gulls, 10 = snakes, 11 = other canids. † Figures in brackets represent predation rates by all medium sized carnivores including red foxes, grey foxes, arctic foxes, skunks, racoons and badgers. Predation rates marked * were calculated using the Mayfield method (Mayfield, 1975), otherwise they were calculated as the ratio of predated nests to total nests. Latin names are presented alphabetically in Table 2.6.

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Harris' sparrow	Northern Manitoba	Tundra	24	?	4.2	1,6-9,11	Jehl (1971)
White-crowned sparrow	Northern Manitoba	Tundra	46	?	5.3	1,6-9,11	Jehl (1971)
Smith's longspur	Northern Manitoba	Tundra	30	0	0	1,6-9,11	Jehl (1971)
Chestnut-collared longspur	Southern Alberta	Meadow	76		47.4	1-4,7-10	O'Grady *et al.* (1996)
Dickcissel	Kansas	Meadow	535	?	45.8, 71.0*	1-4,7-11	Zimmerman (1984)
Field sparrow		Meadow	66	?	36.4	1-4,7-11	Nolan (1963)
Field sparrow	Illinois	Meadow	147	(10.9)	76.2	1-4,7-11	Best (1978)
Grasshopper sparrow	West Virginia	Meadow	51	?	56.7, 62.4*	1-3,7-11	Wray *et al.* (1982)
Savannah sparrow	West Virginia	Meadow	41	?	36.5, 40.0*	1-3,7-11	Wray *et al.* (1982)
Savannah sparrow	New Brunswick	Island	398	0, (0)	50.1, 80.1*	9	Dixon (1978)
Savannah sparrow	Alaska	Meadow	130	?	1.0	1,6-9,11	Miller & Knight (1993)
Vesper sparrow	West Virginia	Meadow	70	?	54.2, 56.6*	1-3,7-11	Wray *et al.* (1982)
Seaside sparrow	Massa-chusetts	Salt marsh	27	0	14.8	1-3,7-11	Marshall & Reinert (1990)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Dark-eyed junco	Utah	Meadow	74	?	32.4	1?,2-4,7-11	Smith & Andersen (1982)
Dark-eyed junco	Arizona	Meadow	55	?	30.9, 53.0*	2,3,7-11	Martin (1993)
Black-eared wheatear	Spain	Maquis	53	18.9, 34.0*	32.1, 50.8*	1,7-10	Suárez & Manrique (1992)
Thekla lark	Spain	Maquis	61	?	45.9, 63.4*	1,7-10	Suárez & Manrique (1992)
Lesser short-toed lark	Spain	Maquis	43	?	55.8, 76.3*	1,7-10	Suárez & Manrique (1992)
Water pipit	Wyoming	Tundra	76	?	36.8	1?,7-9,11	Verbeek (1970)
Meadow pipit	Poland	Meadow	?	?	47.0*	1,5,7-9	Halupka (1998)
Meadow pipit	Holland	Meadow	?	?	3.8*	1,5,7-9	Beintema & Müskens (1987)
Sage sparrow	North-western United States	Maquis	36	?	25.0, 32.9*	1-4, 7-11	Rotenberry & Wiens (1989)
Sage sparrow	Idaho	Maquis	17	?	44.0, 60.0*	1-4, 7-11	Reynolds (1981)
Sage thrasher	Idaho	Maquis	49	?	31.0, 55.0*	1-4, 7-11	Reynolds (1981)
Brewer's sparrow	North-western United States	Maquis	78	?	14.1, 14.8*	1-4, 7-11	Rotenberry & Wiens (1989)
McCown's longspur	Colorado	Meadow	78	?	52.6	1?,2-4,7-11	With (1994)

Species	Location	Habitat	*n*	Predation by foxes† (%)	Total predation (%)	Predators	Source
Lapland longspur	Alaska	Tundra	94	?	52.6, 53.3*	6-9	Custer & Pitelka (1977)
Orange-crowned warbler	Arizona	Meadow	90	?	33.3, 49.9*	2,3,7-11	Martin (1993)
Virginia's warbler	Arizona	Meadow	26	?	30.8, 42.0*	2,3,7-11	Martin (1993)
Red-faced warbler	Arizona	Meadow	30	?	40.0, 48.2*	2,3,7-11	Martin (1993)
Worm-eating warbler	Arkansas	Meadow	19	?	26.3, 50.1*	1-4,7-11	Martin (1993)
Ovenbird	Arkansas	Meadow	14	?	28.6, 51.1*	1-4,7-11	Martin (1993)
Black-and-white warbler	Arkansas	Meadow	14	?	21.4, 29.0*	1-4,7-11	Martin (1993)
Meadowlark	Illinois	Meadow	262	?	51.2	1-4,7-11	Roseberry & Klimstra (1970)
Skylark	England	Meadow	88	?	54.5	1,5,7-9	Delius (1965)
Skylark	Holland	Meadow		?	43.2*	1,5,7-9	Beintema & Müskens (1987)

Foxes have not been implicated as important predators of passerine nests elsewhere in their range. Miller & Knight (1993) recorded very low nest predation rates in a sample of 130 savannah sparrow *Passerculus sandwichensis* nests, with only a single nest being lost throughout the whole three-year study period. Their study site in central Alaska is within the range of both arctic and red foxes. They suggested that the low nest predation rate on their study site compared with other studies could be attributed to the absence of racoons and, in particular, snakes, which have been shown to the most important predators in warmer parts of the sparrow's breeding range (Best, 1978; Wray *et al.*, 1982).

In southern Michigan, Rogers & Caro (1998) found that nest predation rates on song sparrows *Melospiza meloda* decreased following the re-introduction of coyotes in the area. They suggested that this decrease was brought about by a decrease in the abundance of racoons as a result of aggressive interactions with coyotes, in line with the meso-predator release hypothesis. This study suggests, therefore, that racoons are the most important predator of song sparrow nests in their study site. Vickery *et al.* (1992) found that striped skunks were largely responsible for high nest predation rates (58.0%, $n = 60$) in grassland nesting passerines in Maine. They found that the rate of nest predation in a plot was positively correlated with measures of skunk insect foraging activity. The authors concluded that nest predation was incidental, or in other words, a fortuitous capture of an unexpected prey item not leading to any change in search pattern. Incidental nest predation may explain how relatively large predators such as foxes and skunks can exert a high predation rate on small and dispersed passerine nests, a prey type of low profitability.

In summary, it is clear that foxes have the potential to be an important predator of ground-nesting passerine nests. Although the nests of passerines are small and occur at low densities, therefore representing a food item of relatively low profitability to foxes, they may suffer high predation rates by foxes and other medium sized mammalian egg predators from incidental predation. There are very few studies that identify the predators of passerine nests so it is not possible to determine the relative importance of foxes in most cases.

2.4 Discussion

As a result of the increasing need to manage bird populations for conservation or for harvest in the modern landscape, it has become important to identify the principal nest predators, so that the most appropriate management strategies for increasing bird productivity can be developed. In both Europe and North America, the red fox has

traditionally been considered as one of the most important predators of small game (Darrow, 1947; Tapper, 1991), and as a result foxes have frequently been a prime candidate as the most important nest predator for many bird species.

However, nest predators are very difficult to identify from nest remains, and in many cases, it has not been possible to reliably identify the nest predator. Even modern techniques such as radio-tagged wax filled eggs in nests and photographic techniques have the potential to influence predator behaviour and may therefore give unusual results. Thus, published studies of nest predation may not represent a random sample of nest predation. It is possible that published studies may be biased towards cases of very high nest predation rates or particularly low nest predation rates because they are deemed more interesting by researchers or game managers. Published studies may be biased in other ways. For example, studies on the effect of foxes on duck nest success come largely from the prairie pothole region of North America. Although this region covers a very large area, conclusions drawn from studies in this location may not be applicable in other parts of the red fox's range or in other biomes. Similarly, much of the large scale evidence for the effects of foxes on game-birds comes from Scandinavia, which again sets a locational bias.

It is easier to identify nest predators for species nesting on sandy substrates. Although it has been possible to determine the impact of foxes in several studies of beach nesting waders, considerably less is known about the importance of foxes as nest predators of species nesting in other habitats. In ground-nesting passerines, there are only two studies that have measured the impact of foxes on nest success (both at the same site) and more studies are needed to draw general conclusions.

Having clarified the caveats of making generalisations about the importance of foxes on nest predation, it is clear that red foxes have the potential to be very important nest predators. However, there is considerable between-site variation in the nest success of species such as lapwings, in similar habitats in the presence of foxes, and it is likely,

therefore, that there are a number of site-specific characteristics independent of local fox abundance that influence nest predation rate. Potentially important site-specific characteristics include the relative location and density of the main prey types of foxes, and the density and distribution of nests.

In the next chapter, I compare nest predation rate in lapwings in 6 separate sites in the Lower Derwent Valley in Yorkshire where foxes are common. In a study of lapwing nest success in Sweden, Berg *et al.* (1992) found that crows were the most important nest predator at his study sites where foxes were very rare due to the national sarcoptic mange event. Crows were shown to produce a characteristic spatial pattern of nest success, with higher success in denser groupings of nests as a result of more effective communal nest defence. In the next chapter, I test the hypothesis that crows are still the most important nest predator in an area with high fox activity by comparing the spatial pattern of nest predation with that found in Berg *et al.* (1992).

Table 2.6 List of wader and ground-nesting passerine species in nest predation studies

Common name	Scientific name
American avocet	*Recurvirostra americanus*
Avocet	*Recurvirostra avosetta*
Black-eared wheatear	*Oenanthe hispanica*
Black-necked stilt	*Himantopus mexicanus*
Black-tailed godwit	*Limisa limosa*
Brewer's sparrow	*Spizella breweri*
Buff-breasted sandpiper	*Tryngites subruficollis*
Chestnut-collared longspur	*Calcarius ornatus*
Common sandpiper	*Actitis hypoleucos*
Curlew	*Numenius arquata*
Dark-eyed junco	*Junco hyemalis mearnsi*
Dickcissel	*Spiza americana*
Dunlin	*Calidris alpina*
Eurasian dotterel	*Charadrius morinellus*
Field sparrow	*Spizella pusilla*
Golden plover	*Pluvialis apricaria*
Grasshopper sparrow	*Ammodramus savannarum*
Greenshank	*Tringa nebularia*
Harris' Sparrow	*Zonotrichia querula*
Killdeer	*Charadrius vociferus*
Lapland longspur	*Calcarius lapponicus*
Lapwing	*Vanellus vanellus*
Least sandpiper	*Calidris minutilla*
Lesser short-toed lark	*Calandrella rufescens*
Long-billed curlew	*Numenius americanus*
McCowan's longspur	*Calcarius mccownii*

Common name	Scientific name
Meadowlark	*Sturnella magna*
Mountain plover	*Charadrius montanus*
Pectoral sandpiper	*Calidris melanotos*
Piping plover	*Charadrius melodus*
Red-necked phalarope	*Phalaropus lobatus*
Redshank	*Tringa totanus*
Ringed plover	*Charadrius hiaticula*
Ruff	*Philomachus pugnax*
Sage sparrow	*Amphispiza belli*
Sage thrasher	*Oreoscoptes montanus*
Savannah sparrow	*Passerculus sandwichensis*
Seaside sparrow	*Ammodramus maritimus*
Semipalmated plover	*Charadrius semipalmatus*
Skylark	*Alauda avensis*
Smith's longspur	*Calcarius pictus*
Snipe	*Gallinago gallinago*
Snowy plover	*Charadrius alexandrinus*
Spotted sandpiper	*Actitis macularia*
Stilt sandpiper	*Micropalama himantopus*
Temminck's stint	*Calidris teminckii*
Thekla lark	*Galerida theklae*
Turnstone	*Arenaria interpres*
Vesper sparrow	*Pooecetes gramineus*
Water pipit	*Anthus spinoletta*
Whimbrel	*Numenius phaeopus*
White-crowned sparrow	*Zonotrichia leucophrys*
Wilson's phalarope	*Phalaropus tricolor*
Wilson's plover	*Charadrius wilsonia*

3. Spatial patterns of nest predation in lapwing *Vanellus vanellus* colonies in wet meadows

Summary

1. Lapwings achieved a nesting success of 70.0% in wet meadow habitats in North Yorkshire where foxes were found to be active throughout the nesting season.

2. Nesting success of lapwings was higher for nests with greater numbers of nearest neighbours, an effect thought to be brought about by improved nest defence against carrion crows by the correspondingly higher densities of lapwings. The number of neighbouring nests within 100 m of a nest explained 95.5% of the variation in the probability of surviving nest predation. These results are comparable with those of Berg *et al.* (1992), which were obtained from a study area largely free of foxes. This pattern of nest predation suggests that crows are the most important lapwing nest predators at this site, despite the presence of foxes.

3. A predated nest was more likely to have a predated nearest neighbour than would be expected by chance. This may be caused by site restricted search by predators or may also occur if a group of nests are found in an area where predators are particularly active (close to predator den or nesting site, or close to travel paths) or where predators are more efficient (close to a favoured vantage point for crows, in a small habitat area that helps to concentrate the predator's search or in a habitat that provides inadequate cover or camouflage for nests).

3.1 Introduction

There has been a decline in the abundance of lapwings in Britain since the mid-1980s according to population indices derived from the Common Birds Census (Marchant *et al.*, 1990). From an analysis of British ringing recoveries, it has been shown that adult and

first year survival rates have actually increased since 1960 (Peach *et al.* 1994) suggesting that the population decline is associated with decreased productivity rather than first year and adult survival. Whilst it is acknowledged that changes in habitat and farming practice have reduced the area of available nesting sites and decreased the survival rates of eggs and chicks (e.g. Shrubb, 1990; Lovegrove *et al.*, 199*) predation is also thought to be an important factor reducing productivity.

In Britain, there are many predator species that could potentially take lapwing eggs and chicks. In northern Britain, Baines (1990) found that 46.7% of clutches were taken by avian predators, namely carrion crows *Corvus corone* and black-headed gulls *Larus ridibundus*. No overnight clutch predation was recorded so nocturnal predators such as foxes and other mammalian predators were not thought to be major predators of eggs. Galbraith (1988) also recorded heavy egg loss to predators in Scotland, with 59.3% and 89.4% of eggs lost to predators on arable and rough grazing respectively. Most egg predation had been caused by carrion crows or unknown mammalian predators.

In many studies, nest predation has been shown to be density-dependent, including those that employ experimental manipulations of artificial nests (e.g. Goransson *et al.*, 1975; Picman, 1988; Larivière & Messier, 1998), and comparisons of real nests at different densities (e.g. Dunn, 1976; Zimmerman, 1984; George, 1987). In contrast, there is strong evidence to suggest that the nest predation rate of lapwings is inversely density-dependent with nests at high densities suffering lower predation rates than solitary nests or nests at low densities (Berg *et al.*, 1992; Berg, 1996). This effect is brought about by the increased effectiveness of communal nest defence against crows in large colonies (Elliot, 1985). However, all the evidence for inversely density-dependent nest predation in lapwings comes from studies carried out in Sweden during the late 1980s when a national epizootic of sarcoptic mange was at its peak, and the population of red foxes was greatly reduced (Lindström *et al.*, 1994). Foxes were very rare in these lapwing study sites (Å. Berg, pers. comm.). However, in Britain, foxes are thought to be an important predator of lapwing eggs and chicks (Harold, 1994).

O'Reilly and Hannon (1989) showed that predation on artificial grouse nests was spatially clumped. This effect was brought about by area concentrated search of predators, in particular red foxes that were the most common predators of artificial nests in their study site. Larivière & Messier (1998) also found that at high and intermediate artificial nest densities there was evidence for clumped nest predation by mammalian egg predators. Both foxes and crows have been shown to be able to carry out site restricted search, a behaviour that can lead to clumped and density-dependent patterns of predation (Tinbergen *et al.*, 1967, Macdonald, 1980). However, lapwings nest in very loose colonies, with well separated nests, a 'strategy' that has been shown to reduce nest predation rates by mammalian predators (Tinbergen *et al.* 1967; Taylor, 1976; Shugart & Scharf, 1977; Hogstad, 1995). Foxes have been shown to inflict high nest predation rates in colonies of terns that aggressively defend their nests against intruders (Musgrave, 1993), therefore it is unlikely that foxes are deterred by the anti-predator behaviour of lapwings. As a result, an inversely density-dependent pattern of nest predation would not be expected to be produced by foxes. Instead. foxes would be expected to produce a positively density-dependent, or density-independent pattern of nest predation, depending on the efficacy of the spacing-out of nests as a defence against fox predation.

Studies using artificial and natural nests have shown that proximity to habitat edges sometimes, though not always, has an effect on nest survival (Paton, 1994; Major & Kendal, 1996). Increased nest predation close to habitat edges may be brought about by increased mammalian activity close to habitat edges, a behaviour that has been noted in red foxes (Oehler & Litvaitis, 1996, Chapter 4) or by increased avian predator activity or hunting efficiency at edges (Elliot, 1985; Andrén, 1992). For example, crows search for nests from vantage points that are abundant in some habitat edges such as forest edges, hedgerows and fence lines (Berg *et al.*, 1992). Berg (1996) found that proximity to forest edges had no effect on lapwing nest survival, whilst Berg *et al.* (1992) have shown that lapwing nest predation is significantly higher for nests closer to trees or other perches (though not necessarily habitat edges) suitable for avian predators. High lapwing nest

predation in close proximity to potential crow perching sites would provide additional evidence for the identification of the most influential nest predator.

In order to reduce nest predation effectively, it is important to identify the principal predators responsible. Identifying the predator of grassland nesting waders is very difficult, because in most cases, the only sign that the clutch has been predated is the disappearance of the eggs. The goal of this study is to determine whether or not lapwing nest predation is inversely density-dependent, and in doing so, provide evidence for the identification of the principal nest predator.

3.2 Methods

3.2.1 Study site

The study was carried out in the spring of 1997 from the middle of March to the end of June at seven sites in the Lower Derwent Valley in North Yorkshire (approximately 53°53'N, 0°55'W). Each study site consisted of a near uninterrupted habitat type contained in a single enclosure. All of the study sites, Bank Island (BI), Wheldrake Ings (WI), Thornton Ings (TI), Aughton Ings (AI), Thorganby Ings (THI), North Duffield Carrs (NDC) and the Refuge (RE) were seasonally flooded hay meadows managed by English Nature and local farmers as a nature reserve using summer hay cropping and late summer or autumn grazing to promote good conditions for breeding waders. All these study sites were set in low mixed farmland.

Although there is no policy of fox control on BI, WI, NDC and TI which are managed by English Nature, the surrounding landowners actively control foxes with shooting and dogs, so it is not thought that the area holds atypical fox densities for lowland mixed farming habitats in Britain. There was thought to be particularly high levels of predator control around AI and THI.

3.2.2 Monitoring lapwing nest success

Nests of all waders were located by noting the position of incubating adults with binoculars from a vehicle. Having been found, the position of nests were marked with a one metre metal cane marked with plastic tape positioned ten metres from the nest at an arbitrarily chosen bearing (to help prevent predators learning the location of nests from the location of canes). Wellington boots were always worn when marking or checking nests to avoid leaving scent trails that may be followed by foxes. All of the lapwing nesting sites were visited at least once every three days but usually more frequently. During each visit the number of lapwing adults at the site was counted and the nests were checked by seeing whether or not the adults were incubating their nests. If the adult was not seen on the nest after two visits and the nest was not expected to have hatched, the nest was closely examined. A nest was considered successfully hatched if chicks were seen in the nest, or minute shell fragments were found in the nest lining (Galbraith, 1988; Baines, 1990; Berg *et al.*, 1992). Predated nests were characterised by complete or partial disappearance of eggs. In some predated nests egg remains could be seen near the nest. Also during each visit, the number of broods of chicks were counted. The presence of broods could be frequently revealed by the behaviour of the adults such as brooding where the adult bird could be seen sitting high over chicks, or leading, where the adult would be seen walking across the ground, stopping frequently and making gentle calls (Spencer, 1951). Often it was possible to see the chicks as they moved after the adult bird. The minimum number of broods at a site was estimated by counting the numbers of adults showing parental behaviour. If a male and female lapwing were making chick calls in the same area (less than 20m apart), these would be assumed to calling the same brood of chicks.

3.2.3 Measuring nest density

The location of lapwing nests with respect to other nests and topographical features such as fences and drainage ditches were measured with a 200m tape measure. All

measurements were made after all the nests had either hatched or been predated so that disturbance to the breeding birds was minimised. The position of each nest relative to topographical features was then plotted onto appropriately scaled maps. Distances to other nests, habitat edges, potential avian predator perches and linear features were measured indirectly using these maps.

3.2.4 Monitoring fox activity

At least once every two weeks, and usually more frequently searches were made for fox tracks, scats and kills at each site. Searches were made by slowly walking the perimeters of the study sites, which were usually delimited by fences, and scanning the ground paying particular attention to muddy areas where footprints were most likely to occur. In addition to the perimeter, other locations where fox footprints are commonly found were also checked, including the edges of drainage ditches, along bunds and at the muddy margins of floodwaters. At four of the sites, namely BI, WI, RE and NDC building sand was placed in locations where foxes were likely to pass such as gaps in fences and points of access across flooded drainage ditches. If the sand was kept slightly damp, the footprints of even small animals such as stoats *Mustela erminea* would be easily recognisable. Approximately ten kilograms of sand was spread over an area of a single square metre or less. One of these 'footprint stations' was maintained at WI, four at NDC and three at BI. These were checked and smoothed daily throughout April. Care was taken not to leave any human scent that may deter foxes, and the sand was always smoothed with a flat stick found in the field. In addition, all farm-workers on land adjacent to the study site were interviewed regularly throughout the spring and early summer to determine whether or not they had seen or caught any foxes.

3.2.5 Statistical analyses

Measuring nest predation as the ratio of predated nests to the total number of nests can underestimate nest predation largely because nests that were predated before the start of a

study are harder to find than active nests (Mayfield, 1961). Mayfield (1961, 1975) resolved this problem by considering nest predation as a daily probability of predation *m*, which is calculated by dividing the number of nests lost by the number of nest-days (the total number of days the nests were exposed). The daily probability of nest survival P, known as the 'P-value', is therefore 1- *m*. If the daily probability of survival is assumed to be constant throughout the laying and incubation period, then the overall probability of nest survival can be measured as P^t where *t* is the time taken to lay and incubate a clutch of eggs to hatching. If there is reason to believe that the daily probability of survival is not constant, then data can be grouped into separate periods. For example, if it is thought that nests are more likely to be robbed during the laying phase, a daily survival probability for the laying phase P_{laying} is calculated, and the overall probability of surviving the laying phase is $P_{laying}^{tlaying}$, where *tlaying* is the duration of the laying period. The total probability of survival in this case, is simply the product of the probability of surviving the laying period and the probability of surviving the incubation period. The time taken to lay, incubate and successfully hatch a clutch of lapwing eggs is assumed to be 26 days. The Mayfield measure of the daily probability of survival is in fact the maximum likelihood estimate of the daily probability of survival (Hensler & Nichols, 1981) and therefore has certain statistical properties making it possible to estimate the variance, s^2, using the following formula:

$$s^2 = \frac{\hat{p}(1-\hat{p})}{\sum_{n=1}^{N} days_n}$$

where $\hat{p}$ is the daily probability of survival using Hensler & Nichol's (1981) notation, *N* is the total number of nests, and $days_n$ is the number of days for which nest *n* was exposed (Hensler & Nichols, 1981). All P-values are presented with the standard deviation, *s*, obtained from the above formula. Hensler & Nichols (1981) have presented the following test for the equality of P-values from two populations of nests: Reject Ho, the null hypothesis that $p_1 = p_2$, in favour of the alternative hypothesis $p_1 \neq p_2$ if and only if

$$\frac{|\hat{p}_1 - \hat{p}_2|}{\sqrt{s_1^2 + s_2^2}} > z_{\alpha/2}$$

where $z_{\alpha/2}$ is the upper $\alpha/2$ value for the standard normal distribution. For all tests the significance level is set to $\alpha = 0.05$. For parametric tests the assumptions of normality and heteroscedasticity were tested using the appropriate statistical tests.

3.3 Results

3.3.1 Fox activity

Wheldrake Ings: at one of the footprint stations, fresh fox prints were found on 5 out of the 12 times it was checked throughout the month of April. Five different sets of fox tracks were found in muddy ground in WI at regular intervals throughout the nesting season. A fox was seen in the lapwing colony on two occasions in early June. A vixen with cubs was seen on adjacent farmland by farm-workers, and the breeding den subsequently located approximately 1 km from the nesting site on WI.

The Refuge: the footprint station never yielded any fox prints, but fox prints were found in mud in the middle of the breeding area in early June. There was also evidence of fox activity in a black-headed gull colony adjacent to the lapwing nesting site which included fox tracks and the remains of black-headed gull chicks presumably killed by foxes. The lapwing colony in RE is approximately 1 km from the lapwing nesting site in WI, and although the two areas are largely separated by floodwater there are a number of broad access points into RE from WI, so it is possible that the foxes from WI are also active in RE.

North Duffield Carrs: two footprint stations that were maintained for 20 days over April registered fresh fox prints twice. Some of the footprint stations were washed away by rain and not reset because fox prints were never found in them. On six separate occasions

during the nesting season (April to June) fox prints were found in muddy patches in NDC; one set of these tracks passed within 6m of an active lapwing nest. A pregnant vixen had been caught by terriers in a small wood within 500m of NDC in March, but an adult fox was seen close to the lapwing nesting site twice and on a third occasion was observed trotting along a fence in the site itself.

Bank Island: none of the footprint stations yielded any fox prints, but fresh fox tracks were regularly found in muddy areas found at the edges of the floodwater and the bunds that cross the floodwater. From the 20 April to 8 June fresh fox tracks were found on the main bund eight times showing that foxes regularly searched these narrow (ca. 2m) bunds. The fox was thought to have been responsible for killing an incubating Canada goose nesting on the bund in late April.

Thornton Ings: an adult fox was seen in adjacent rough grassland at the end of March. No foxes were shot by farmers in surrounding farmland during the lapwing nesting season, so it is assumed that at least one fox was active in the vicinity throughout the nesting period.

Aughton Ings: fox prints were seen in muddy ground on one occasion only at the beginning of May. The area of muddy ground was small at this site and this may explain why so few fox tracks were detected. At the end of May and the beginning of June at least one fox was regularly seen on adjacent farmland approximately 1 km from the lapwing colony in AI.

Thorganby Ings: one side of THI was bounded by the River Derwent, the rest of the perimeter was surrounded by heavily keepered land. At least two foxes were shot in this adjacent farmland between November and February, and no evidence for the presence of foxes was found on the site. It is possible, therefore, that foxes never visited this site. In addition all corvid species were regularly shot and trapped in this area.

Stoat tracks were regularly seen in all the footprint stations in WI, NDC, BI and RE, and were seen more frequently than fox tracks.

3.3.2 Factors related to predation rate

In total 116 lapwing nests were monitored throughout the incubation period across all seven sites. Thirty-three of these nests were lost to predators, and only one was lost to other causes, in this case trampling by livestock, making the overall probability of surviving predation nearly 70% (Table 3.1).

Table 3.1. Nest success at different sites in the Lower Derwent Valley, 1997.

Site	Total nests	Nest days	Losses	P	SD	Hatching success (P^{26})
WI	20	360	8	0.9778	0.00777	0.557
BI	9	146	4	0.9726	0.01353	0.486
NDC	35	764	6	0.9921	0.00319	0.815
AI	26	507	8	0.9842	0.00553	0.661
TI	13	288	2	0.9931	0.00489	0.834
THI	7	195	1	0.9949	0.00512	0.875
RE	6	125	4	0.9680	0.01575	0.429
TOTAL	116	2385	33	0.9861	0.00239	0.696

The mean distance to the nearest neighbouring lapwing nest was 44.9 ± 32.4 metres ranging from 12.3 to 153.0 metres. Two measures of nest crowding were made: the number of neighbouring nests within a 100 m radius and the mean distance to the nearest 5 neighbours. The mean number of nests within a 100 m radius was 3.70 ± 2.02 (ranging between 0 and 9), and the average of the mean distance to the 5 nearest neighbours was 84.0 ± 45.5 metres. A summary of these data are presented in Table 3.2 below. It has been shown by Berg *et al.* (1992) that the risk of lapwing nest predation is higher for nests that are closer than 50 m to trees or other perches suitable for avian predators.

Potential avian predator perches included trees, bushes and fence-posts. Although the daily probability of nest survival was greater for nests far away from trees and other perches as expected, the difference was not significant at alpha equals 0.05 (one-tailed test, $z = 1.51$, $P = 0.065$). The distance of each nest to the nearest linear feature (hedgerow, fence, drainage ditch) or habitat edge (edge of copse or stand of trees, edge of floodwater) was also measured for each nest. The daily probability of surviving predation was significantly higher for nests further away (>20 metres) from linear features or habitat edges (Figure 3.1).

Table 3.2 Summary of nest spatial data. All measurements are metres ± standard deviation. NND denotes the distance to the nearest neighbouring nest. Crowding was measured as the mean distance to the nearest five neighbouring nests. The results of a Kruskal-Wallis test show that there are significant differences in all the measurements except NND between sites.

Site	Mean NND	Mean crowding	Mean distance to habitat edges	Mean distance to perches
BI	49.6 ± 20.32	136.6 ± 29.0	23.8 ± 33.8	98.7 ± 24.0
NDC	53.2 ± 43.8	92.6 ± 59.4	30.2 ± 19.4	80.9 ± 33.7
AI	32.0 ± 15.6	62.9 ± 22.5	25.5 ± 16.6	72.3 ± 27.6
WI	40.0 ± 25.9	75.5 ± 34.4	83.4 ± 35.22	113.0 ± 36.9
THI	66.6 ± 32.8	96.7 ± 30.9	37.91 ± 19.8	95.1 ± 33.1
TOTAL	44.9 ± 32.4	84.0 ± 45.5	36.4 ± 29.7	88.0 ± 35.0
H	9.06	19.65	26.49	16.12
d.f.	4	4	4	4
P	0.060	0.001	<0.001	0.003

Similar to the results of Berg *et al.* (1992) there was a strong positive correlation between the number of neighbouring nests and nest survival (Figure 3.2). The number of nests within 100 m of the nest site explained 95.5% of the variation in mean daily survival rates. Although the number of close neighbours and the distances to habitat edges and linear features were not related (Kruskal-Wallis tests: distance to linear features and habitat edges, $H = 6.49$, $d.f. = 7$, $P = 0.48$), it was not possible to rule out the potentially

confounding effects of site which had significantly different mean numbers of nearest neighbours between sites (one way ANOVA, $F = 4.93$, $d.f. = 4$, $P = 0.001$). All the study sites included in the above analyses are far enough apart (> 1 km) to be considered to be influenced by different predators. It is possible that there are significantly different numbers of predators between sites, for example, there was particularly intense fox and corvid control around THI.

Figure 3.1 Daily probability of survival for lapwing nests within 20 metres of habitat edges and linear features and nests further than 20 metres from habitat edges and linear features. Nests further than 20 metres from habitat edges and linear features had a significantly higher success rate (two-tailed test, $z = 2.09$, $P < 0.05$).

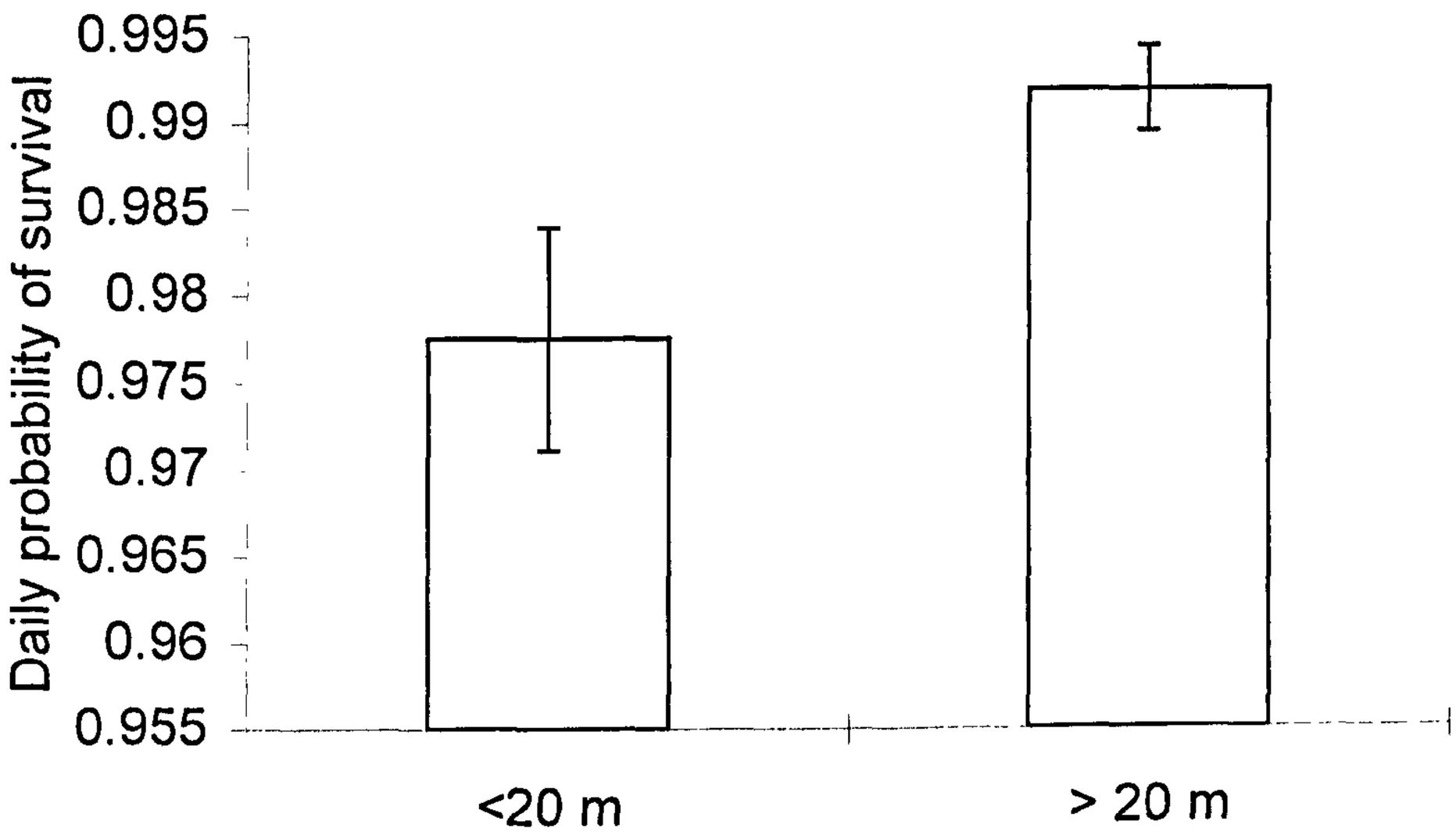
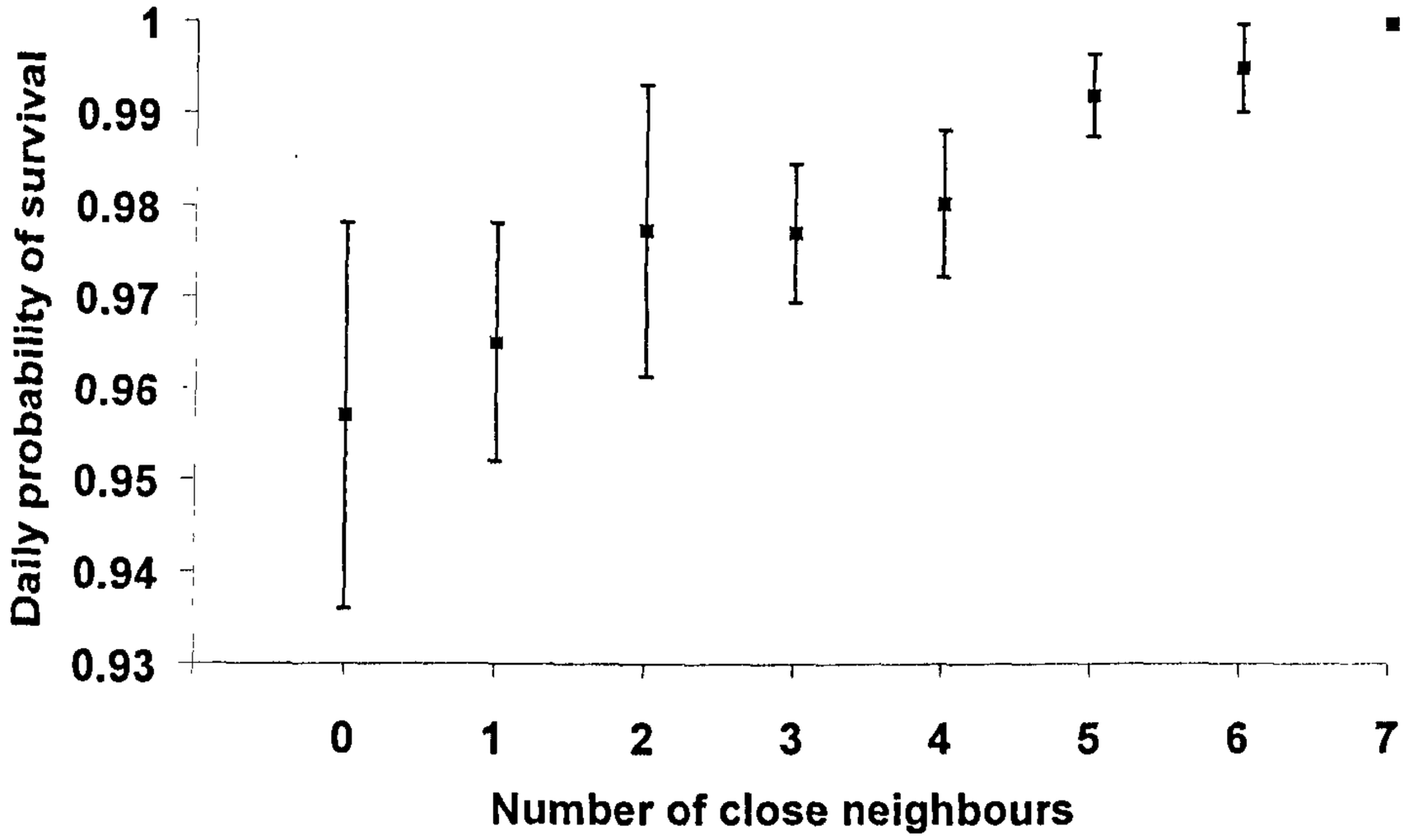


Figure 3.2 Daily probability of surviving predation in lapwing nests with 0 to ≥ 7 close neighbours (nests within 100m of the nest site). A linear regression analysis showed a significant positive correlation between the number of nests within 100m and the daily probability of surviving predation (t = 471.57, n = 8, P < 0.001, R^2 = 95.5%).



In order to account for the potential confounding effects of site a logistic regression model was fitted to the data to predict the probability of nest success. The predictors included the distance to linear features and habitat edges, the distance to perches, the number of near neighbours (within a 100 m radius) and site. The logistic regression confirms that the number of nearest neighbours is an important factor influencing nest predation (Table 3.3), but suggests that the proximity to habitat edge/ linear features does not significantly affect the probability of nest failure when differences across sites have been taken into account. This analysis also shows that proximity to perches had no influence on nest success in this study.

Table 3.3 Results of logistic regression analysis of factors affecting nest predation. (-2 Log-likelihood = 74.90; Test that all slopes are zero: $G = 22.423$, $d.f. = 7$, $P = 0.002$).

Predictor	Coefficient	SD	Wald statistic	*P*
Constant	-2.030	1.052	3.720	0.054
Number of near neighbours	0.624	0.193	10.406	0.001
Distance to edge (m)	0.029	0.016	3.265	0.071
Distance to perch (m)	0.003	0.009	0.098	0.754
Site	-	-	9.941	0.094

A chi-squared test was carried out in order to determine whether or not there was any association between predation events in nearest neighbours. The 2 × 2 contingency table (Table 3.4) shows that there is a significant association between predated nests, in other words, a predated nest is more likely to have a predated nearest neighbour than would be expected by chance.

Table 3.4 Contingency table showing the observed frequencies of predated and successful nests with successful and predated nearest neighbours. Predated nests were more likely to have a predated neighbouring nest than would be expected by chance (chi- squared test with Yates' correction for continuity; $\chi^2 = 10.87$, d.f. =1, $P < 0.01$).

	Predated neighbour	Successful neighbour
Predated	18	14
Successful	15	55

3.4 Discussion

The overall nest predation rate of lapwings in this study was 30%, somewhat lower than lapwing nest predation rates reported in similar grassland habitats (Table 3.5), in areas with similar predators. It is interesting to note that high lapwing nest predation rates (43%) have been recorded on Orkney solely due to avian predators (Cuthbert, 1987), namely common gulls *Larus canus* and hooded crows *Corvus corone*. Although rats and feral cats are found on Orkney, the more notorious egg predators including foxes, stoats and weasels are all absent from Orkney and cannot, therefore, have contributed to nest loss in this case.

The results of this study show that despite the evidence for regular fox activity at most sites, nest predation is significantly lower for nests with more nearest neighbours, suggesting that avian predators (in particular carrion crows) are the most important lapwing egg predators at this study site. This finding agrees with the results of Baines' (1990) study of lapwing nest predation, which was also carried out in northern England. Baines regularly observed foxes around his study site, but did not record any over-night nest predation events showing that nest loss was largely due to diurnal predators.

Even in relatively dense nesting groups of lapwings the nests are widely separated. The mean distance to the nearest neighbouring nest was 44.9 ± 32.4m. The lack of a positive density-dependent pattern of nest predation at this site suggests that the observed lapwing nest separation distances are sufficiently far apart to prevent high nest predation rates by foxes. An increase in the fragmentation of nesting habitats may have important implications for the population dynamics of a species that suffers higher predation rates at low densities. If nesting habitat fragmentation results in smaller groups of nesting birds, the corresponding decrease in efficiency in protection from avian predators may result in an increase in nest predation. However, it is not yet established whether or not habitat fragmentation limits group size. Other factors, such as habitat quality or recruitment limitation may also be important determinants of local nest density.

Table 3.5 Nest predation of lapwings in grassland and arable.

1. Baines (1990), 2. Galbraith, (1988), 3. Berg *et al.* (1992), 4. Shrubb (1990), 5. Cuthbert (1987), 6. Beintema & Müskens (1987), 7. Glutz von Blotzheim *et al.* (1975), 8. Matter (1982).

% nests predated	n	Main predators	Foxes present?	Habitat	Source
76%	109	Carrion crows, black-headed gulls	Yes	Improved pasture	1
47%	347	Carrion crows, black-headed gulls	Yes	Unimproved pasture	1
53%	96	Carrion crows, black-headed gulls	Yes	Unimproved meadow	1
52%	78	Carrion crows, black-headed gulls	Yes	Improved meadow	1
25%	88	Carrion crows, black-headed gulls	Yes	Arable	1
50%	152	Crows, unknown mammals	Yes	Unimproved pasture	2
58%	135	Crows, unknown mammals	Yes	Arable	2
14%	870	Crows	Low density	Mixed farmland	3
9%	2734	?	Yes	Arable	4
20%	1021	?	Yes	Grassland	4
43%	75	Hooded crows, Common gulls	No	Rough grazing	5
44%	?	Gulls, crows, mustelids	Yes	Wet meadow / pasture	6
23.5%	1803 (eggs)	?	Yes	Farmland	7
26%	?	?	Yes	Arable and grassland	8
30%	116	Carrion crows	Yes	Wet meadow and pasture	This study

Although the inverse density-dependent pattern of nest predation indicates that crows are the principal nest predator, there was no effect of proximity to avian predator perches on nest success, an effect that was found in Berg *et al.*'s (1992) study. Since there was no significant difference in the numbers of nearest neighbours for nests close to and far away from potential perches ($t = -0.32$, $n = 91$, n.s.) this cannot be used to explain why there

was no effect of perch proximity as expected. It is possible that some perch sites were incorrectly identified, and that fence-posts, for example, were not as suitable as a searching post as trees. Furthermore, it is possible that particular vantage points were favoured, perhaps because they were closer to the avian predator's nesting site or they offered greater cover from the anti-predator behaviour of lapwings.

A comparison of the hatching success of nests less than 20 m and greater than 20 m from linear features and habitat edges suggested that nests closer to these features suffered a higher predation rate, however, the logistic regression analysis revealed that this result was confounded with site. When differences between sites were taken into account, the proximity of nests to linear features and habitat edges could no longer be used to confidently predict nest success. At one of the sites, BI , four lapwing nests were found on narrow bunds (approximately 3 m across) that traversed the floodwater. All of these nests were less than 2 m from the edge of the floodwater and all of these nests were predated, presumably by foxes whose footprints were seen along the length of the bunds. These nests heavily influenced the results shown in Figure 3.1, and if the same analysis is repeated without these nests then the there is no significant effect of habitat edge/ linear feature on nest success. Nests on narrow strips of habitat may be particularly susceptible to predation by terrestrial predators because the predator's movement can be confined to a small area which can be searched more efficiently. Indeed, Crabtree *et al.* (1989) found that the predation rate of gadwall nests by mammalian predators was significantly higher on narrow dikes.

Predation on lapwing nests was shown to be spatially aggregated or, in other words, a predated nest was more likely to have a predated nearest neighbour than would be expected by chance alone. There are a number of possible explanations for this observation. This pattern may be brought about by site restricted search by the predator (foxes or crows) following nest encounter which can lead to an increased probability of neighbouring nests being predated (Hill, 1984b; Larivière & Messier,1998). Aggregated nest predation may also be caused if a group of nests are found in an area where predators

are particularly active or efficient. For example, all lapwing nests found on bunds at BI were predated because foxes regularly searched these narrow habitats (see Chapter 4). Although proximity to any potential avian predator perch did not influence lapwing nest success it is possible that lapwing nests found in areas near favoured crow perch sites may experience higher predation rates which would lead to aggregated nest predation around these sites. The fact that more than one predation event rarely occurred in any one night does not preclude site restricted search as a potential mechanism leading to clumped nest predation: both foxes and carrion crows have been shown to be able to remember the location of previously encountered prey (Croze, 1970; Macdonald, 1976). These predators may resume searching in areas where they had previously encountered nests in previous bouts of foraging.

It is not known how foxes respond to the encounter of lapwing nests or the anti-predator behaviour of adult lapwings. Although the results from this study suggest that foxes are not important predators of lapwing nests, it is possible that lapwing chicks are more susceptible to predation by foxes. Other sites with different characteristics may suffer higher predation rates by foxes. In the next chapter, I describe the nocturnal behaviour of foxes foraging in lapwing nesting colonies.

4. The activity of foxes *Vulpes vulpes* and other nocturnal predators at lapwing *Vanellus vanellus* nesting sites

Summary

1. Of all the nocturnal predators foxes were the most frequent visitors to lapwing colonies with at least 73% of nocturnal bouts of alarm calls by lapwings elicited by foxes.

2. Foxes visited sites with either nesting and/ or brooding lapwings for a mean of 641 ± 489 seconds per visit, and lapwings responded to the presence of foxes with alarm calls lasting on average for 153 ± 223 seconds.

3. Foxes were seen to visit two of the three arable sites seven times out of fifteen observations for a mean of 126 ± 198 seconds per visit. The nest success at these two sites were 100% and 94%. At a wet meadow site foxes were seen to visit twice out of six observations for an average of 153 ± 343 seconds, and the nest success at this site was 47%.

4. Bouts of alarm calls directed at foxes lasted significantly longer when more broods of chicks were present due to the increased time that foxes spent in the immediate vicinity of breeding lapwing and their broods.

5. There is a positive trend in the duration of fox activity at different sites and the overall density of breeding ground-nesting birds.

4.1 Introduction

In most studies of the nesting success of lapwings, carrion crows have been identified as the major egg predator (Cuthbert, 1987; Galbraith, 1988; Baines, 1990; Berg, 1992). However, a few studies have suggested that mammalian predators are also important. Following a fox and corvid removal campaign at a site on the north coast of Norfolk, lapwing breeding success was seen to increase from fifteen fledged young from 148 pairs to 140 fledged young from 226 pairs (Harold, 1994). In Germany, a study of the nesting success of lapwings has identified foxes as nest predators using remote cameras (Elsner & Blüdhorn, pers. comm.). Two other studies in Europe have indicated that small mustelids were the principal nest predators. In Denmark, Iversen (1986) showed that American mink *Mustela vison* and polecats *Mustela putorius* predated at least 40% of all eggs (n = 80). In a large scale study of wader nest success in Dutch grasslands, Beintema & Müskens (1987) found that the nest predation rate of lapwings and other waders was negatively correlated with vole abundance, suggesting that vole predators, especially small mustelids, were important predators of wader nests when their main prey was scarce.

Foxes, American mink and other small mustelids are all present at the Lower Derwent Valley study site. Even though the spatial pattern of lapwing nest predation suggests that crows were responsible for the majority of lapwing egg losses in 1997, other predators may have contributed to nest loss without obliterating the inversely density-dependent pattern of nest predation. Since foxes appear to rely on aural cues while hunting some prey types such as small mammals and earthworms (Macdonald, 1980), lapwing nests may be more susceptible during the hatching stage when the emerging chicks start to call. Lapwing chicks may be targeted by mammalian predators more than nests during the incubation phase, because they may generate more noise or scent and are therefore easier to detect.

As well as foxes, mammalian lapwing egg and chick predators in Britain include stoats *Mustela erminea* and weasels *Mustela nivalis* (Tapper, 1976), American mink (Day & Linn, 1972), rats *Rattus norvegicus* (Møller, 1983), hedgehogs *Erinaceus europaeus* (Kruuk, 1964; Yalden, 1976; Tapper, 1992) and badgers *Meles meles* (Anon, 1981) which have all been known to prey on the eggs of other bird species. Indeed, lapwings have been seen to show anti-predator responses to hedgehogs (Heim, 1951) and stoats (Lynes, 1910; Coward, 1920). Nocturnal avian predators may also be important: a study of the nesting success of common terns *Sterna hirundo* in the United States revealed that great horned owls *Bubo virginianus* and black-crowned night herons *Nycticorax nycticorax* were responsible for the majority of egg and chick predation (Nisbet & Welton, 1984). It is possible that barn owls *Tyto alba*, tawny owls *Strix aluco* and grey herons *Ardea cinerea* may be predators of lapwing chicks in Britain, though there are no reports of these species even eliciting anti-predator responses from lapwing colonies.

Vickery *et al.* (1992) found that the predation rate of grassland nesting passerines by the striped skunk, a well known mammalian egg predator in North America, was positively correlated to indices of skunk invertebrate-foraging activity. This lead to the notion that nest predation was incidental, i.e. nest encounter was a fortuitous event that did not change the predator's foraging behaviour. In this case, the rate of nest predation was shown to be 58.0% overall. Incidental nest predation is a process that may reduce the effectiveness of nest spacing as a strategy for reducing nest loss to mammalian predators. Clearly, an important factor determining the rate of incidental nest predation is the time the predator spends foraging in the vicinity of nests. Foxes would be expected to spend more time in areas of high prey density, and as a result, higher rates of incidental nest predation by mammalian predators would be expected in areas of high prey density.

In this study there are two main objectives: 1) to estimate the activity of different nocturnal predators at lapwing colonies and to determine the relative importance of foxes as predators of lapwing eggs and chicks, and 2) to determine whether or not the duration of fox foraging activity at lapwing colonies is influenced by the abundance of other

ground-nesting birds in adjacent habitats. In this study, the intensity of nocturnal predator activity was compared across seven contrasting lapwing nesting sites: four of the sites were associated with high densities of other ground-nesting bird species, the remaining three only supported nesting lapwings.

4.2 Methods

4.2.1 Study site

The study was carried out in the spring of 1998 from the beginning of April to the end of June at seven sites in the Lower Derwent Valley in North Yorkshire (approximately 53°53'N, 0°55'W). Each study site consisted of a near uninterrupted habitat type contained in a single enclosure. Four of the study sites, Bank Island (BI), Wheldrake Ings (WI), Thornton Ings (TI) and North Duffield Carrs (NDC) were seasonally flooded hay meadows managed by English Nature and local farmers as a nature reserve using summer hay cropping and late summer or autumn grazing to promote good conditions for breeding waders. The remaining three sites, the Escrick road arable (ERA), East Cottingwith arable (ECA) and the North Duffield arable (NDA) were all sown with sugar beet. All these study sites were set in similar lowland mixed farming land. Although there was no policy of fox control on BI, WI, NDC and TI which are managed by English Nature, the surrounding landowners actively control foxes with shooting and dogs. The spring of 1998 was characterised by particularly heavy rainfall which caused unusually late and repeated extensive flooding of the meadow sites which with the exception of Thornton Ings caused delayed and disrupted breeding attempts by the lapwings and other waders that usually nest at these sites.

4.2.2 Nocturnal observation

Forty-four nocturnal observations were carried out over the study period across the seven sites totalling to almost 200 hours of observation (Table 4.1). Observations usually lasted

for 5 hours starting just before dusk and were made from either permanent wooden hides, portable cloth hides or from a vehicle. The number of nocturnal observations differed between sites for several reasons. The target was a minimum of six observations per site, however, this was not achieved for ERA, NDC and ECA. The ERA lapwing 'colony' was found relatively late in its incubation period, and there was a limited number of days before all the nests had hatched and the site vacated by all lapwings. Due to the large size and extent of flooding at NDC it was very difficult to get close to concentrations of nesting lapwings, and viewing conditions tended to be very poor. As a result, observations at this site were abandoned after four attempts. No nocturnal predator activity was detected at ECA in five nights of observation, so this site was abandoned in favour of sites such as BI and WI where fox activity was much higher. During observations, the portable hide or the vehicle were always placed downwind of the site so that the observer's scent would not alert foxes on the site. The fixed hides were occasionally upwind of the study site, but since foxes were regularly observed from these hides, this was not considered a problem.

An image intensifier (Omega II, Omega Night Vision Systems) was used to observe the lapwing nesting sites at night. A million-candle spotlight with an infra-red filter was used during the first few observations at a different site and this increased the range and quality of viewing dramatically. However, it was noted that when the infra-red beam was shone directly at a fox it would look into the light and then run away. This happened on several occasions so it was decided to abandon the use of the spotlight. Although the vast majority of visible light is blocked out by the filter and foxes are not thought to be able to see infra-red, the dull red glow perceptible to the human eye may be enough to disturb foxes.

Table 4.1 The number and duration of nocturnal observations

Site	Number of observations	Hours of observation
TI	6	29.5
NDA	11	50.2
ERA	4	18.2
BI	8	34.4
ECA	5	23.2
NDC	4	18.8
WI	6	24.8
TOTAL	44	199.2

Foxes and other nocturnal mammalian predators have been observed to elicit particular anti-predator responses from lapwings and redshank that include alarm calls and dive-bombing (Lynes, 1910; Coward, 1920; Heim, 1951; Spencer, 1951; Grosskopf, 1959; Hodson, 1962). Despite the quality of the image provided by the night vision equipment, sometimes it was not possible to detect predators either because there was heavy mist and little moonlight or because the vegetation was tall enough to obscure the predator.

The distinctive alarm calls of the lapwing were used as an indicator of the presence of a predator, and where possible individual alarm calls were counted as they were made, or where not possible (i.e. when fox behaviour was being recorded whilst the lapwings were calling) the start and stop of bouts of alarm calls were noted with the Dictaphone. Redshank and curlew also make alarm calls in response to mammalian predators (Cramp & Simmons, 1983) and the start and finish times of bouts of alarm calls of these species were also recorded.

Two measures of fox foraging effort were made during the nocturnal observations: the first measure was the total time that the fox spent in a particular site, measured from the time that the fox was first detected to the time the fox was deemed to have left the site (i.e. moved into another enclosure), the second measure was the time spent by lapwings alarm calling and mobbing the fox. Errors in the estimates for fox stay times may be incurred if the fox was not detected soon after it first entered the site or if it was difficult

to determine when the fox had left the site, however, it is thought that such errors occurred rarely as the fox was usually seen entering and departing nesting sites. The duration of lapwing alarm calls provided a good estimate of the time spent by the fox in the close vicinity (approximately 100 metre radius) of nests or broods of lapwing chicks, and it was possible to measure this accurately as the alarm calls of lapwings are loud and very distinct.

Ducks, geese and coots were common at Bank Island, Wheldrake Ings and North Duffield Carrs and any sounds of distress or escape from these species were also recorded, although it was not assumed that these sounds were necessarily associated with the presence of a predator.

4.2.3 Monitoring the abundance of lapwings and their chicks and determining nest success at lapwing colonies

Each site was visited every day or once every two days, and the number of lapwings, the number and status of nests, and the number of lapwing broods were noted at each visit (see section 3.2.2 for nest checking protocol). Counts of other waders and waterbirds on the wet meadow sites (BI, NDC, WI and TI) were made each month by the English Nature estate workers who managed the sites. Counts of other bird species on the arable sites (NDA, ERA and ECA) were made almost daily.

4.2.4 Statistical analyses

A significance level of 0.05 was used for all statistical tests. When carrying out two-sample t-tests and ANOVA the assumptions of normality and heteroscedasticity of data were tested and the appropriate data transformations were carried out where necessary.

All error bars show ± standard deviation unless otherwise indicated.

Nest success was measured using the Mayfield method (Mayfield, 1961,1975) which uses the ratio of the number of nests lost to the number of nest-days (the total number of days

the nests were exposed) to calculate a daily probability of survival, P. The time taken to lay, incubate and successfully hatch a clutch of lapwing eggs was assumed to be 26 days. Hatching success was measured as P^{26}. Standard deviations for the daily probability of survival are obtained using the method of Hensler and Nichols (1981), which are outlined in section 3.2.5.

4.3 Results

4.3.1 Nest and bird density

The number of breeding waders varied considerably between sites. Lapwings were the only waders found on the arable sites (NDA, ERA and ECA), but breeding redshank, curlew and snipe were also found on the wet meadow sites (Table 4.2). Three of the wet meadow sites, namely BI, WI and NDC, contained a large amount of floodwater throughout the breeding season which attracted many breeding waterfowl (Table 4.3). All of the wet meadow sites experienced flooding, and this was particularly severe for BI and WI which became completely inundated during the last week of April and the first week of May. Table 4.2 shows the change in the area of nesting and feeding habitat available to lapwings and other waders at each site as the water levels changed. Wheldrake Ings also experienced an unusual drop in water levels in mid June due to an unscheduled drainage of the site via a sluice system. By the 10th of May some lapwings had already returned to WI and BI, less than a week after the return to normal water levels, and were seen displaying over the sites. The maximum numbers of territorial lapwing counted at BI, WI and NDC was 12, 20 and 30 respectively (Table 4.2) though these may be underestimates due to the difficulty of detecting feeding lapwings in the long vegetation. At BI only 2 pairs of lapwing actually nested on the site, the other lapwings present were brooding chicks hatched from an adjacent arable field to which access had not been granted.

Table 4.2 The number of breeding waders per site

Site	Area of wader habitat (ha)	No. of territorial lapwings	No. of lapwing nests marked	No. of territorial redshank	No. of territorial curlew	No. of territorial snipe
NDA	6.04	30	15	0	0	0
NDC	9.81 - 34.16	30*	7	24	16	24
ECA	4.74	16	8	0	0	0
ERA	8.96	12	3	0	0	0
BI	0 - 13.59	12*	2	12	4	10
WI	0 - 35.83 (16.95)	20*	0	28	12	26
TI	8.60 - 10.47	14	8	8	16	4

*Maximum number seen during breeding period

Table 4.3 The number of other breeding ground-nesting birds at each site

Site	Area of water (ha)	No. of territorial ducks	No. of territorial coot	No. of territorial moorhen	Other territorial birds
NDA	0	0	0	0	2 partridges*
NDC	4.83 - 39.37	529	200	32	25 geese 1000 black-headed gulls
ECA	0	0	0	0	1 pheasant* 1 partridge*
ERA	0	0	0	0	6 pheasant* 6 partridge*
BI	8.63 - 22.22	120	60	22	0
WI	0 - 64.38 (19.38)	388	260	30	58 geese
TI	0 - 1.87	6	0	2	2 geese

* Minimum number of birds seen on the study site.

By the time the floodwaters had receded sufficiently from WI to allow nesting, the height of the vegetation in the meadow was already becoming too tall for ideal lapwing nesting conditions (Shrubb, 1990), so although there were at least fifteen lapwing seen displaying on the nineteenth of May, a non-breeding flock of thirty birds was seen on the site on the twenty-eighth of May (birds that had presumably given up attempting to breed) and by the eighth of June only four lapwing were flushed from the site. However, two or more broods of lapwing chicks were detected on the site on the seventh, ninth and twenty-third of June, suggesting that chicks were brought on to the site from elsewhere. NDC never completely flooded and territorial lapwing numbers varied between twenty to thirty birds.

4.3.2 Activity of nocturnal predators at lapwing nesting sites

In 199.2 hours of nocturnal observation at the seven sites 44 bouts of lapwing alarm calls were heard. Table 4.4 shows the frequency and duration of these bouts of alarms at each site. The large majority of these bouts of alarm calls (73%) were associated with foxes i.e. foxes were seen in the lapwing colony and the response of the lapwings were clearly directed at a fox. Out of the remaining 27% of alarm bouts only one of these was definitely attributable to a predator other than a fox, when a pair of lapwings were seen dive-bombing a small animal in short grass close to the observation post. For the rest of the alarm bouts in this category no predator could be seen either because of poor viewing conditions due to weather or the predator was too far away or obscured by vegetation. There is no significant difference between the mean duration of alarm bouts that were associated with foxes and those where the predator remained unidentified (t =0.68, d.f.= 17, n.s.). The only other mammalian predator actually seen in a lapwing colony at night during these observations was the European badger, which was observed walking close to an area with lapwing chicks at BI, but did not elicit any alarm calls or mobbing response from the adult lapwings.

Table 4.4 Frequency and duration of nocturnal lapwing alarm calls.

Site	No. of bouts per hour of observation	Mean duration of bouts ± s.d. (seconds)	Proportion of bouts associated with foxes	Proportion of bouts where no predator seen
NDA	0.100	519.0 ± 588.8	0.60	0.40
NDC	0	-	-	-
ECA	0.086	75.0 ± 21.2	0	1
ERA	0.493	126.8 ± 42.2	0.67	0.33
BI	0.349	78.4 ± 65.6	1	0
WI	0.564	135.4 ± 107.3	0.29	0.56
TI	0.068	141.5 ± 139.3	1	0
All Sites	**0.210**	**153.3 ± 222.8**	**0.73**	**0.27**

Badger tracks were also seen crossing TI and ECA. At both sites the tracks followed almost a straight line, along the edge of the field at ECA and following a track at TI, suggesting that the badgers were only passing through these sites rather than foraging in them. On two occasions mammalian predators were seen during the day: a rat was observed walking away from the grass verge that surrounded NDA, and a stoat was seen being mobbed by an adult lapwing at ERA. On the latter occasion, a single adult lapwing was seen giving alarm calls and dive-bombing a stoat which was seen running across the arable field, an event which lasted approximately thirty seconds.

Barn owls and tawny owls were occasional seen or heard in the vicinity of the lapwing colonies but were never seen to elicit alarm calls from adult lapwings. For the nocturnal observations where owl activity was monitored the duration of observation was divided into 595 ten minute intervals. Barn owls were detected in only 10 of these ten minute intervals and tawny owls detected in 13 of the 595 intervals. On two occasions tawny owls were observed hunting in NDA where they were seen dropping into the grass

surrounding the arable field, presumably catching small mammals (no lapwing chicks were present when this hunting behaviour was observed).

During these nocturnal observations no other nocturnal predators were seen foraging in the vicinity of lapwing nesting or chick rearing sites, however, during a nocturnal observation at WI in the spring of 1996 a grey heron was seen to be mobbed by several lapwings as it walked through the middle of a lapwing nesting area.

4.3.3 Factors affecting the time spent by foxes in and around lapwing nesting and chick rearing sites

Foxes were observed at all sites except NDC and ECA, however, foxes were certainly present at NDC because fresh fox tracks were regularly seen around the site. Foxes may also have been present at ECA because on several occasions lapwings were heard responding to an unseen nocturnal predator with alarm calls, however, fox tracks were never found at ECA even though the site was regularly checked for predator tracks. It was decided to exclude the data obtained from NDC because a) foxes were not observed although they were known to regularly visit the site b) it was never possible to observe much of the site accessible to foxes due to the extensive floodwater and c) observation positions were either exposed and therefore possibly perceptible to foxes or too far away for a good view of the site.

The intensity of fox activity at each site may be measured as the total time that the fox spent at each site controlled for the total duration of observation. It may have be easier to detect foxes in large sites and observe them for longer because larger sites provided a larger uninterrupted view, and for this reason the measure of fox intensity is controlled for the area over which the fox could be detected. Using this measure of fox activity it can be shown that foxes spend more time in sites of high bird density (Figure 4.1).

The mean duration of individual visits by foxes to the different sites was 641 ± 489 seconds (n=18) with a maximum of 1380 seconds (twenty-three minutes). The mean visit duration corrected for area was greater in sites with large numbers of breeding ducks and waders (Figure 4.2), however, since there was a lot of variation in stay times within sites, the mean stay times were not significantly different between sites (one way ANOVA, $F_{4,17} = 0.65$, n.s.).

Figure 4.1 The intensity of fox activity at sites with different numbers of breeding ground-nesting birds

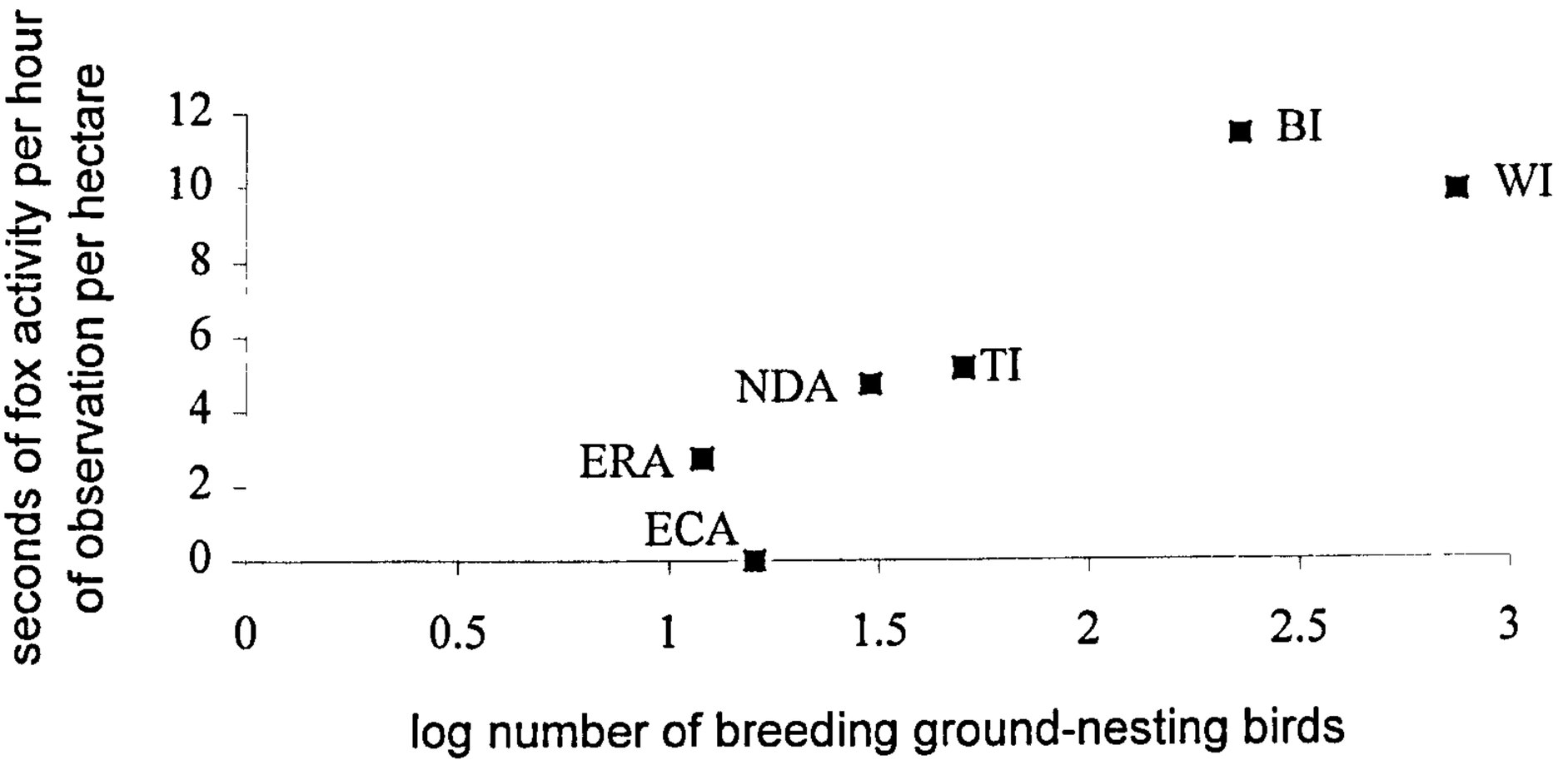


Figure 4.3 shows the intensity of alarm calling measured as the seconds of alarm calling per hour of observation against the log total number of breeding ground nesting birds. Although the overall amount of nocturnal alarm calling is higher in sites with many breeding ground- nesting birds (mostly ducks), the relationship is not clear. The mean time that foxes spent among breeding lapwings per visit (measured as the duration of bouts of alarm calls) was 212 ± 184 seconds ($n = 18$) with a maximum of approximately 600 seconds (ten minutes).

Figure 4.2 The mean stay time per hectare per visit against log number of breeding birds

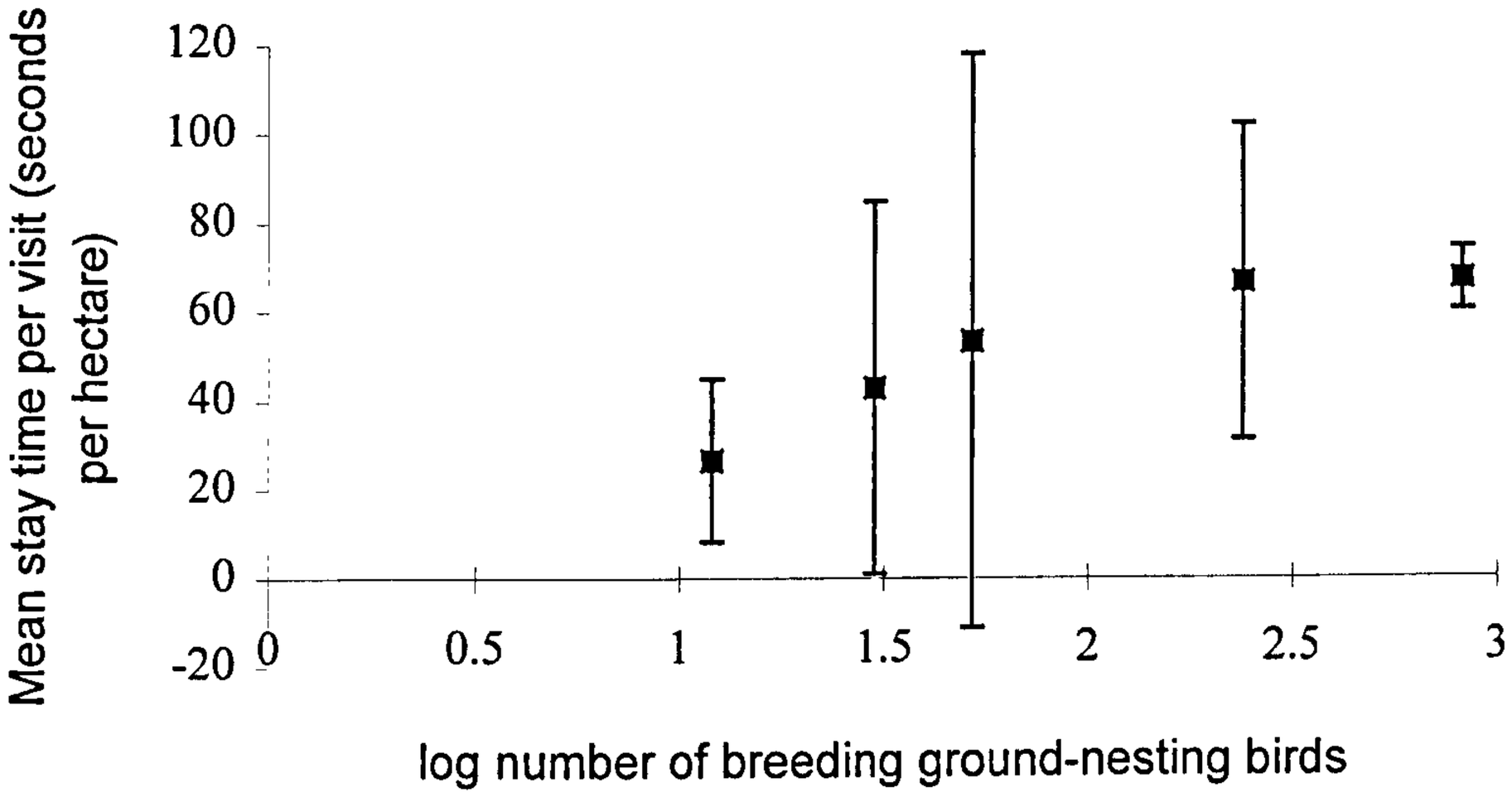
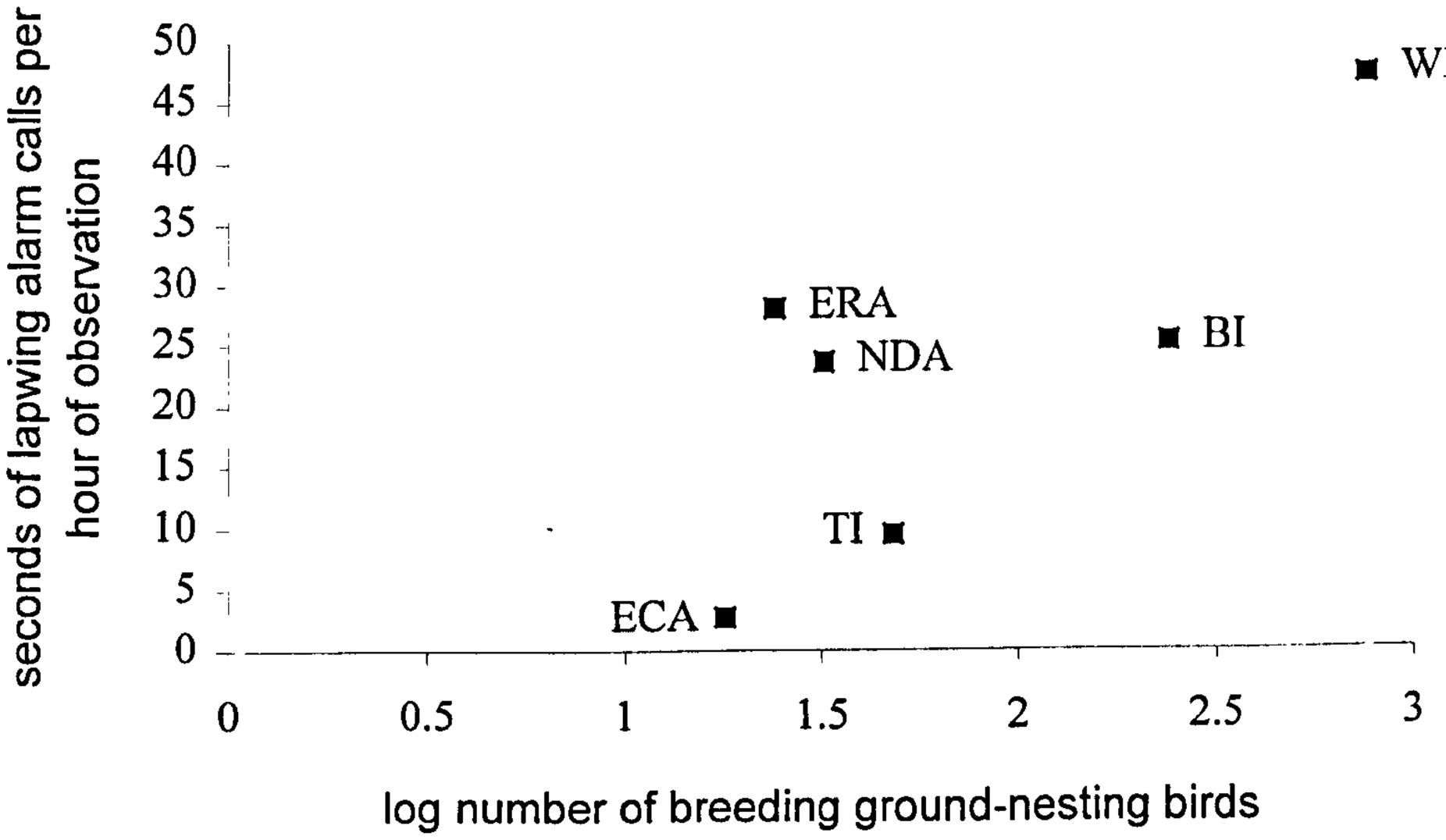


Figure 4.3 Total duration of lapwing alarm calls per hour of observation against log number of breeding birds



Foxes spent significantly more time in the immediate vicinity of breeding lapwings when there were more broods of lapwing chicks present (Table 4.5). It is not possible to control for the effects of date in this model because the number of broods is related to the date of observation, i.e. more broods will be seen towards the end of the breeding season as more clutches of eggs hatch. It is possible, therefore, that other date related factors are influencing stay times.

Table 4.5 ANCOVA for the effect of site on log lapwing alarm duration (in response to the presence of foxes) with the number of lapwing broods present as a covariate

Source	*d.f.*	Adj. MS	*F*	*P*
Site	4	28600	1.07	0.412
Minimum number of lapwing broods present	1	139563	5.24	0.041
Error	12	26622		
Total	17			

3.3.4 Fox activity and nest success

At the arable sites ECA, ERA and NDA foxes were seen for 0, 25 and 29 seconds per hour of observation respectively. Nest success at these sites was very high: no nests were lost at ECA and ERA and only a single nest out of fifteen was lost to predators on NDA showing that foxes found few if any nests on these arable sites. It was difficult to make detailed observations of fox movement on the arable fields where the most concentrated lapwing nesting colonies were located because there was little contrast between the image of the fox and the bare soil background when using the night vision.

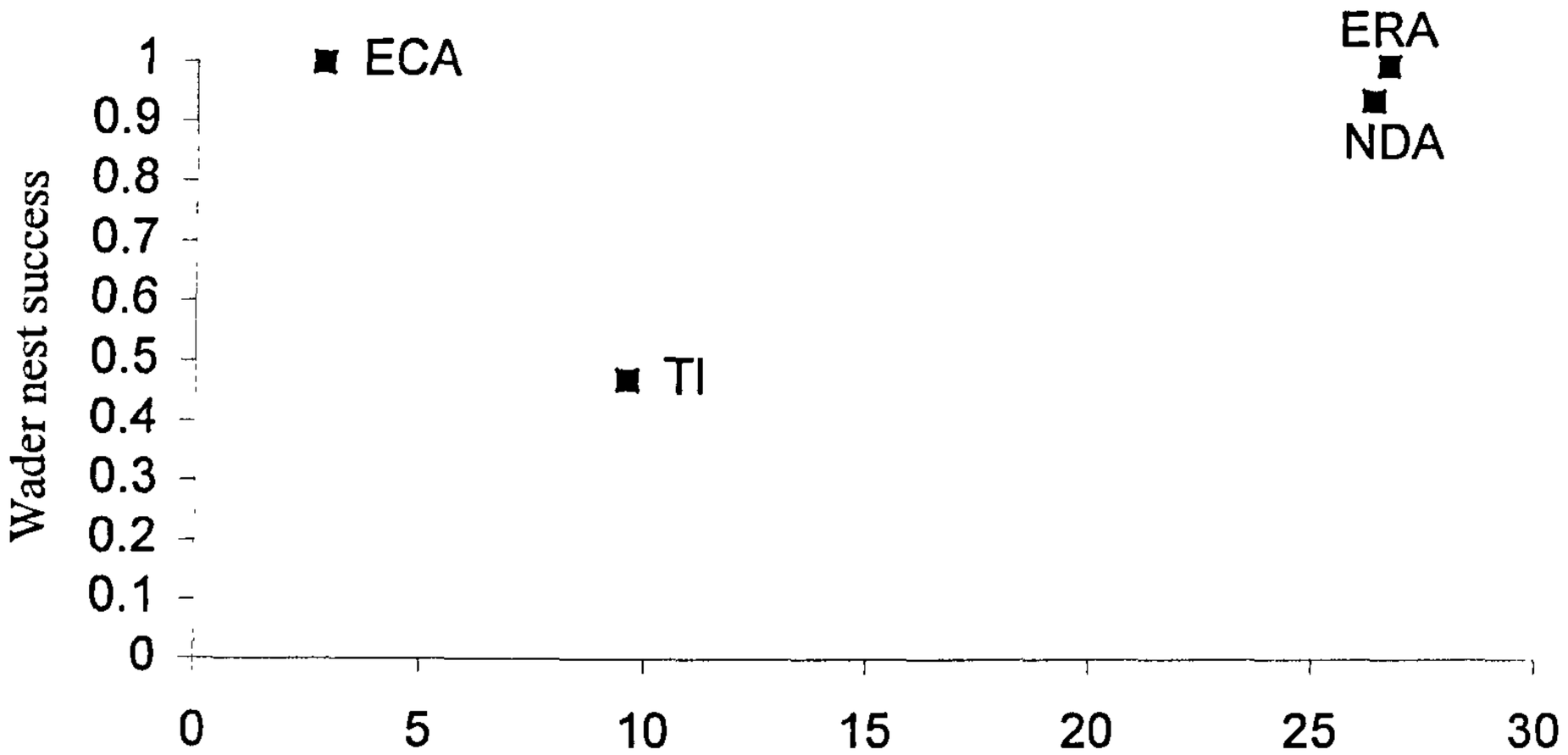
On only two occasions was it possible to observe lapwing nests being predated by foxes, and both of these were at BI on the same night. In the first predation event the fox was

seen walking slowly in a series of short distances interspersed with pauses and turns with its head close to the ground. The fox was being mobbed by a lapwing, but did not appear to be bothered by it. The last movements prior to the first nest encounter was a sharp turn followed by a 2.3 metre walk followed by a momentary pause and then a pounce onto the position of a lapwing nest. On the second predation event the fox had been moving in the same direction at a walk for 16 seconds when it began to be mobbed by a single lapwing. The fox continued to walk in the same direction for a further 8 seconds when it made a right angled turn and darted approximately 2.5 metres into the grass and was seen to pick something up in its jaws. Close examination of the two lapwing nests the following day confirmed they had both been predated. These were the only two nests found on the site.

In one 2.1 ha section of TI (delimited by a sparse hawthorn hedge) where two lapwing nests were present, a fox was observed to forage within this site for 66 seconds on one night in April and for 476 seconds (approximately 8 minutes) on another night in the same month. On both occasions at least four lapwings were observed to respond to the presence of the fox by vigorous alarm calling and dive bombing. Although the fox was seen to spend much of the time within at most 50 metres of the nests they were not robbed. In total there was 12 seconds of fox activity per hour of observation at TI and four out of seven wader nests located in the observation area were predated.

There appears to be no association between the time spent by foxes and other nocturnal predators in the immediate vicinity of a lapwing colony (measured as the total duration of all bouts of alarm calling per hour of observation) and nest success (Figure 4.4). However, with data on nesting success available for only four of the sites (the other sites were unsuitable for nesting lapwings due to the unusually late flooding) it is not possible to draw any firm conclusions on the effect of foraging duration on nest success.

Figure 4.4 The duration of nocturnal alarm calls and the nesting success of lapwings at four sites



4.4 Discussion

4.4.1 Nocturnal predator activity

At least 73% of nocturnal lapwing alarm call bouts were directed to foxes suggesting that of all the potential nocturnal predators known to be present around the study sites foxes were the most frequent visitors to lapwing colonies at night. In the remaining 27% of alarm call bouts it was not possible to detect the predator either because it was too misty, too far away or obscured by vegetation in all but one of the cases where the lapwings were clearly directing anti-predator behaviour (alarm calling and dive-bombing) at a predator small enough to be obscured in grass less than 30cm in height. Given that the duration of alarm calls elicited by foxes was not significantly different from the duration of alarm calls elicited by unseen predators it is plausible that foxes were responsible for generating more than 73% of alarm call bouts. These results show that other nocturnal predators spend considerably less time in lapwing colonies than foxes, and although the time a predator spends in the vicinity of lapwing nests is not necessarily proportional to

the rate of egg predation by that predator, the results suggest that other nocturnal predators are even less important lapwing egg predators than foxes. This is in contrast to the findings of other studies: Iversen (1986) considered mink *Mustela vison* and polecats *Putorius putorius* to be amongst the most important lapwing nest predators at a Danish nesting site. Although polecats are not found in North Yorkshire (Blandford & Walton, 1991) mink were occasionally seen around the wet meadow sites. In a study of wader nesting success in Dutch grasslands Beintema & Müskens (1987) found that the nest predation rate of lapwings and several other wader species was inversely correlated with the abundance of voles (*Microtus*) thought to be caused by prey switching by mustelids.

4.4.2 Factors affecting the time spent by foxes in and around lapwing nesting and chick rearing sites

A number of authors have found nest predation to be density dependent (e.g. Tinbergen *et al.*, 1967; Reitsma, 1992; Larivière & Messier, 1998) but it is not known by which mechanism nest predators such as foxes change their behaviour in response to nest density. One possible behavioural mechanism that may lead to density dependent nest predation is to increase the time spent foraging in areas of high nest density. The results from this study suggest that foxes spend more time foraging in sites with large numbers of breeding waders and waterfowl. However, due to the large number of observations required to yield data of adequate accuracy on fox activity, information from only six sites was available, which means that these findings should be treated with some caution. Similarly, the total time spent in the vicinity of lapwing breeding colonies (measured as the duration of all alarm calls directed at a fox per hour of observation) appears to increase as the overall density of all ground-nesting birds at the site increases, but again these results should be treated with caution for the same reasons. Macdonald (1980) found that when foxes are foraging for earthworms they will visit fields of high earthworm density significantly more frequently than fields with lower earthworm density, showing that foxes are indeed able to adjust foraging effort to prey density.

This study provides evidence to show that per visit foxes spend more time in the immediate vicinity of lapwing breeding colonies when there are more broods present. Even though chicks tend to freeze and lie quiet when disturbed, they are probably easier for foxes to detect than nests because some chicks in the brood were often heard to call despite the presence of an intruder and alarm calls by the parent. It is possible that an increase in cues denoting the presence of prey such as chick calls may cause foxes to spend more time searching in the immediate vicinity of those cues even if the fox does not actually encounter any chicks. It is possible that increased foraging times in areas of relatively high chick density may lead to greater rates of chick predation by foxes.

4.4.3 Fox activity and nest success

Because flooding prevented lapwings from breeding in WI and greatly disrupted breeding at BI, and because no fox activity data was obtained from NDC only the remaining four sites yielded data on both nesting success and fox activity, far too few to test hypotheses concerning the relationship between fox activity and nest success.

It is interesting to note that nesting success in the arable sites was very high (> 90%) despite the fact the foxes were known to be regular visitors of ERA (two visits in four observations totalling 476 seconds) and NDA (five visits in eleven observations totalling 1298 seconds).

The lapwing colonies on the arable sites enjoyed significantly higher nest success than those on the wet meadow sites (arable 96%, wet meadow 31%, $z = 4.03$, $n = 54$, $P < 0.05$) which agrees with the results of Baines (1989) and Shrubb (1990), but again the sample size was too small to determine whether or not this was due to differences in fox activity because there was only a single meadow site where it was possible to measure both nest success and fox activity. However, lapwing nesting success in wet meadow sites including WI, BI, TI and NDC in the previous year have been much higher (total nest success 70%) even though field signs suggested that foxes visited these sites regularly.

5. The search behaviour of red foxes foraging in grassland wader nesting sites

Summary

1. The nocturnal search behaviour of foxes was observed in five different wader nesting sites in the Lower Derwent Valley in the spring of 1998.

2. Foxes were observed to elicit alarm calling a mobbing behaviour from lapwings. On eight occasions, foxes maintained ongoing, direct travel paths whilst being mobbed by adult lapwings in nesting habitats. On six occasions, foxes appeared to respond to the lapwings behaviour by initiating a convoluted travel path that restricted the foxes search to a limited area (<0.5ha - 3ha). The duration of convoluted search in the presence of alarm calling lapwings ranged from 104 seconds to greater than 600 seconds (mean 459 ± 302.9 seconds)

3. Foxes were sometimes seen to use systematic, zigzag search paths when moving along bunds.

4. Foxes frequently followed linear topographical features found around wader nesting sites including bunds, the edge of floodwater, tyre-tracks in the grass, and ditches.

5.1 Introduction

Although birds and their eggs form a relatively small part of the red foxes diet (Lloyd, 1980), foxes have been shown to have a large effect on the nest success of many ground-nesting bird species, including several species of wader (Pienkowski, 1984; Rimmer & Deblinger, 1990; Patterson *et al.*, 1991; Paton, 1995). In a study of piping plover nest predation on a Massachusetts beach, fox tracks in the sand suggested that fox located nests through 'accidental encounters or during systematic searches through nesting

habitat' (MacIvor *et al.*, 1990). It has been shown that 'accidental' nest encounters by mammalian egg predators can result in high nest predation rates (Vickery *et al.*, 1992).

For a terrestrial predator foraging for static and often cryptic prey items such as birds nests, predation rate will be largely determined by the predator's nest detection ability, and the predator's search tactic, since the 'handling time' (the time taken to attack, subdue and consume a prey item) will be small compared to the search time. Due to their largely nocturnal activity patterns, foxes have rarely been observed foraging in ground-nesting bird breeding sites, and it is not known what type of search patterns they adopt or how they alter their search behaviour in response to the presence of nesting birds.

Many animals, including red foxes, have been shown to alter their search behaviour in response to cues associated with prey or prey encounter. Sonerud (1988) observed two sequential encounters between a red fox and a brooding hen game birds. In both encounters, the fox was observed to ignore the distraction display of the hen, and carry out a site restricted search in the vicinity of the point at which the hen was flushed. Macdonald (1980) showed that foxes could restrict their search to small areas (20 × 30 m or less) when hunting for earthworms. In this case, site restricted search was not brought about by increasing turn angles or shortening move lengths in response to prey encounter, a behaviour noted in other species (e.g. Smith, 1974). Instead, foxes may have maintained site restricted search by recognising patch boundaries or continuously re-orientating towards stimuli such as sound generated by the prey. The ability to carry out site restricted search in response to any factor associated with the presence of ground-nesting birds' nests may have important consequences for nest predation rate. Henry (1977) has described the search behaviour of red foxes scavenging for food-items on a forest floor, which included what appears to be site-restricted search behaviour. He also noted that foxes spent significantly less time investigating urine marked sites on the ground, a behaviour which can lead to a more systematic exploration of a search area. A zigzag search pattern has been shown in badgers *Meles meles* searching for prey (probably worms) along the lee-side of hedgerows using spool and line tracking (J.

Brown, unpublished data), and there are numerous anecdotal accounts of foxes adopting the same search pattern along hedgerows. A predator capable of systematically searching nesting habitats could potentially inflict heavy nest losses.

A number of nest predation studies have shown that proximity to habitat edges can be an important factor in reducing nest survival (see Paton, 1994 for a review). Avian predators such as common crows, for example, may create this edge effect because they can efficiently scan for nests from perch sites common in forest edges, hedges and fences (e.g. Berg, 1996). It has been proposed that mammalian predators may also generate an edge effect by foraging along 'travel lanes', linear topographical features (Marini *et al.*, 1995), and indeed, there is some evidence that red foxes associate with habitat edges at certain times of year (Oehler & Litvaitis, 1996).

The purpose of this study is a), to determine the response of red foxes to the anti-predator behaviour of adult lapwings, b) to describe the search path of foxes with respect to nests and topographical features, and c) to quantify the basic movement parameters (speed, straight line distances moved, turn angles and pause duration) of foxes foraging in wader nesting habitats.

5.2 Methods

5.2.1 Study site

The study was carried out in the spring of 1998 from the beginning of April to the end of June at seven sites in the Lower Derwent Valley in North Yorkshire (approximately 53°53'N, 0°55'W). Four of the study sites, Bank Island (BI), Wheldrake Ings (WI), Thornton Ings (TI) and North Duffield Carrs (NDC) were seasonally flooded hay meadows managed by English Nature and local farmers as a nature reserve using summer hay cropping and late summer or autumn grazing to promote good conditions for breeding waders. These sites remained partially flooded throughout spring and attracted

many nesting ducks and geese. The borders of the flood water at BI and WI were characterised by tall patches of reed sweet-grass *Glyceria maxima* which reached a height of around 60 cm or more by mid June. The remaining three sites, the Escrick Road arable (ERA), East Cottingwith arable (ECA) and the North Duffield arable (NDA) were all individual fields sown with sugar beet and held no floodwater and contained no waterfowl, only breeding lapwings.

5.2.2 Recording fox search behaviour

Forty-four nocturnal observations were carried out over the study period across the seven sites totalling to almost 200 hours of observation. The protocol for nocturnal observation is presented in Section 4.2.2.

Fox behaviour was recorded directly onto a pocket Dictaphone. As the fox was observed details of the fox's movement and hunting behaviour were recorded continuously. A fox's movement was described by gait (stationary, walking, trotting or running) number and sharpness of turns relative to its previous direction (straight ahead (*c*. 0°), soft turn (<90°), medium turn (*c*. 90°), sharp turn (>90°) and reverse direction (*c*. 180°)) were recorded as well as the duration of pauses between straight line movements. The position of the fox relative to conspicuous features in the site was continuously recorded. As all these data were recorded in real time on a Dictaphone it was possible to measure the duration of particular behaviour types back in the laboratory. Straight line distances moved by a fox could be estimated by dividing the time taken to travel between subsequent pauses or turns by the estimated speed. Foxes moving at a walk, trot and a gallop were assumed to be travelling at 0.38, 2.70 and 6.00 metres per second (Lloyd, 1980; Macdonald, 1980).

5.3 Results

The night vision equipment proved to be a useful tool for observing nocturnal animal behaviour from distances of up to 400 metres. However, the quality of the image was greatly reduced by weather conditions such as mist and rain, reducing the effective range of observations to 50 metres or less, and was less effective when the moon and stars were obscured by heavy cloud, reducing the range to around 200 metres. Using the night vision scope, foxes and hares could be clearly seen against a background of vegetation, but mammals were very difficult to see against a background of bare soil, reducing the effective range of the night scope to less than 100 metres on the sugar beet fields prior to the crop's emergence. Foxes were observed seventeen times at five different locations throughout the spring of 1998. Table 5.1 presents the dates and duration of fox observations at each site. Foxes frequently moved out of sight during observations either by obscuring themselves in tall vegetation or moving out of range of the night vision scope. However, it was usually possible to confirm the presence and approximate location of a fox by the alarm calls made by lapwings and other waders allowing an accurate measurement of the time spent by a fox in any given site.

Fox search behaviour was characterised by a series of straight line movements separated by pauses and turns. Within lapwing nesting habitats, foxes were observed moving at different gaits including walking, trotting and running. The mean straight line distance moved when walking was 3.0 ± 3.1 metres ($n = 96$) and was considerably shorter than the mean straight line distance moved when trotting (31.4 ± 31.7 metres, $n = 61$), which in turn were shorter than the mean straight line distance moved when running (93.6 ± 72.1 metres, $n = 23$). In between successive straight line distances, foxes sometimes paused for a few seconds (mean 1.3 ± 3.0 seconds, $n = 140$) in order to sniff the ground or look around. Pauses were sometimes, but not always, associated with a change in direction. The frequency distribution of turn categories was roughly symmetrical with a mode of around zero degrees. The proportion of time spent walking, trotting and running varied considerably with site and date. For example, at ERA on April 29th, the fox never

slowed to below a trot suggesting that it was not foraging, simply travelling. In contrast, the fox that regularly visited BI (identified by its bent tail) spent up to 70% of its time in the site walking.

Table 5.1 Summary of fox observations

Site	Date	Duration of direct observation (s)	Fox stay time (s)
TI	21-April	66	66
TI	27-April	567	852
ERA	29-April	62	121
NDA	6-May	42	42
NDA	12-May	340	460
ERA	15-May	140	355
BI	18-May	182	609
WI	19-May	53	1140
BI	26-May	495	1264
BI	28-May	162	558
BI	1-June	47	271
BI	2-June	240	1380
WI	7-June	66	1260
BI	8-June	585	1352
WI	9-June	199	1020
NDA	11-June	26	116
NDA	16-June	70	600

5.3.1 Evidence for site restricted search

On at least six occasions convoluted search paths were carried out in the immediate vicinity of broods of lapwing chicks or nests by at least four different individuals, suggesting that these search patterns were sometimes triggered by cues from incubating lapwings or their chicks (Table 5.3). It is not known which factors initiated or terminated convoluted search paths in foxes, but it is certain that nest encounter was not necessary to start such search patterns because convoluted search paths were never preceded by prey capture. On seven occasions, however, foxes did not respond to the presence of breeding lapwings (denoted by lapwing alarm calls) by adopting convoluted search paths, and were

not seen to make changes in their direction of movement of greater than a soft turn (Table 5.2).

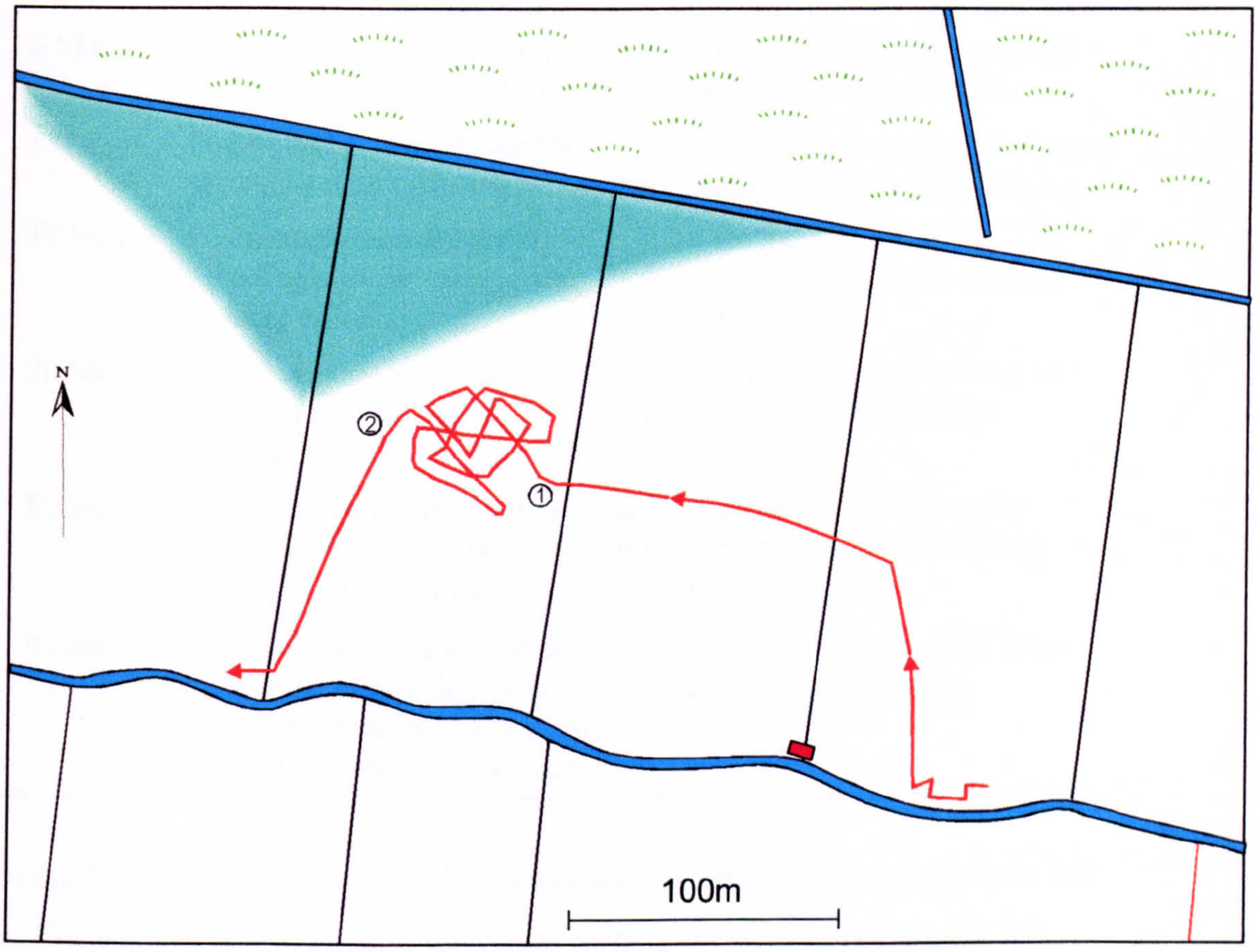
In order to determine whether or not there was any real difference in search effort between search tactics categorised as convoluted, and search tactics categorised as direct, the time spent foraging per hectare was compared between the two categories. The minimum number of hectares occupied by foxes was calculated by overlaying the estimated travel path of the fox onto a map marked with hectare grid cells. Using this method, it was possible to estimate the time spent foraging per hectare for eight direct travel paths, and six convoluted search paths. The median time spent per hectare on direct travel paths (21.1 s ha^{-1}) was significantly less than that of convoluted search paths (191.1 s ha^{-1}) showing that foxes did not always respond the same way to the presence of alarm calling lapwings (Mann-Whitney test, $W = 36.0$, $P = 0.0024$).

shows the duration of six examples of apparent site restricted search behaviour in which foxes adopted convoluted search paths. In all cases the foxes always moved at a walk whilst visible during these periods, though for part of three of the observations it was not possible to make detailed descriptions of movement behaviour because the fox was too far away or obscured by vegetation. In the remaining cases foxes were observed clearly enough to determine that they spent all their time walking. Figure 5.1 shows the estimated search path of a fox at TI on the 27th of April. Between points 1 and 2 along the fox's search path shown in Figure 5.1 the fox spent 436 seconds searching by moving back and forth changing direction frequently, keeping within an area of less than 1 hectare. Two lapwing nests were situated within this area, but were not located by the fox. One of these nests successfully hatched the whole clutch, the other was abandoned due to flooding.

The search paths depicted in the following figures were estimated by eye, and although much of the path may be considered to be accurate to within ± 5m (subjective error estimate) there were some periods in which the fox disappeared from view. In order to

make the figures easier to interpret I have not broken the search path for short disappearances (less than two minutes) by assuming the fox was moved directly from the point where it disappeared to the point where it subsequently re-appeared. In two cases foxes were observed to carry out convoluted search paths but were too distant to discern all turns and pauses, once on the 27th of April at TI between the points 1 and 2 shown in Figure 5.1, and once on the 8th of June between points 3 and 4 shown in Figure 5.3. In these cases I have depicted hypothetical search paths that lie within the limits of the observed search paths (i.e. they cover a similar area).

Figure 5.1 The search path of a fox at TI on the 27th of April.



Flood water

Glyceria

Search path of fox

Hide

Table 5.2 Direct paths through lapwing nesting habitats

Site	Date	Fox activity	Lapwing activity
ERA	29 April	Fox seen crossing site on two separate occasions (10 seconds and 51 seconds), both times the fox was running with just one pause seen on the first occasion.	Six lapwing alarm calls on the first occasion, and two on the second.
NDA	6 May	Fox trotted along field margin for 40 seconds without pausing.	No calls from the 11 pairs of nesting lapwing in field.
ERA	15 May	Fox trotted across site for 150 seconds without pausing or turning.	Six lapwings mobbed fox and alarm called continuously.
WI	19 May	Fox trotted through lapwing brooding area for 40 seconds, pausing twice.	Two pairs of brooding lapwing gave alarm calls for 40 seconds
BI	26 May	Fox seen running through lapwing brooding area (44 seconds), without pausing.	Continuous alarm calling and mobbing from a pair of lapwing.
BI	8 June	Fox seen running through lapwing brooding area (79 seconds), without pausing, and one turn of 90°.	Twenty seven alarm calls from two pairs of brooding lapwing.
WI	9 June	Fox seen running and trotting through large brooding area for nearly six minutes, making only three pauses and no sharp turns.	Continuous alarm calls from at least six lapwings.

At BI on the 2nd of June, a fox remained within an area of less than 2.5 ha for at least 889 seconds. The fox was seen at position one on the search path shown in Figure 5.2 and then re-appeared at position two 195 seconds later, and then disappeared from sight. The continued presence of the fox in that area was revealed by vigorous alarm calling from two pairs of lapwings with broods of chicks, which made 278 alarm calls over a period of 694 seconds. At WI on the 7th of June at least two pairs of lapwings were heard giving alarm calls to a fox that was seen close to a lapwing brooding area a few minutes before the lapwings started calling. The lapwings made 165 distinct alarm calls over a period of 270 seconds from an area of no greater than four hectares.

Figure 5.2 The search path of a fox at BI on the 2nd of June.

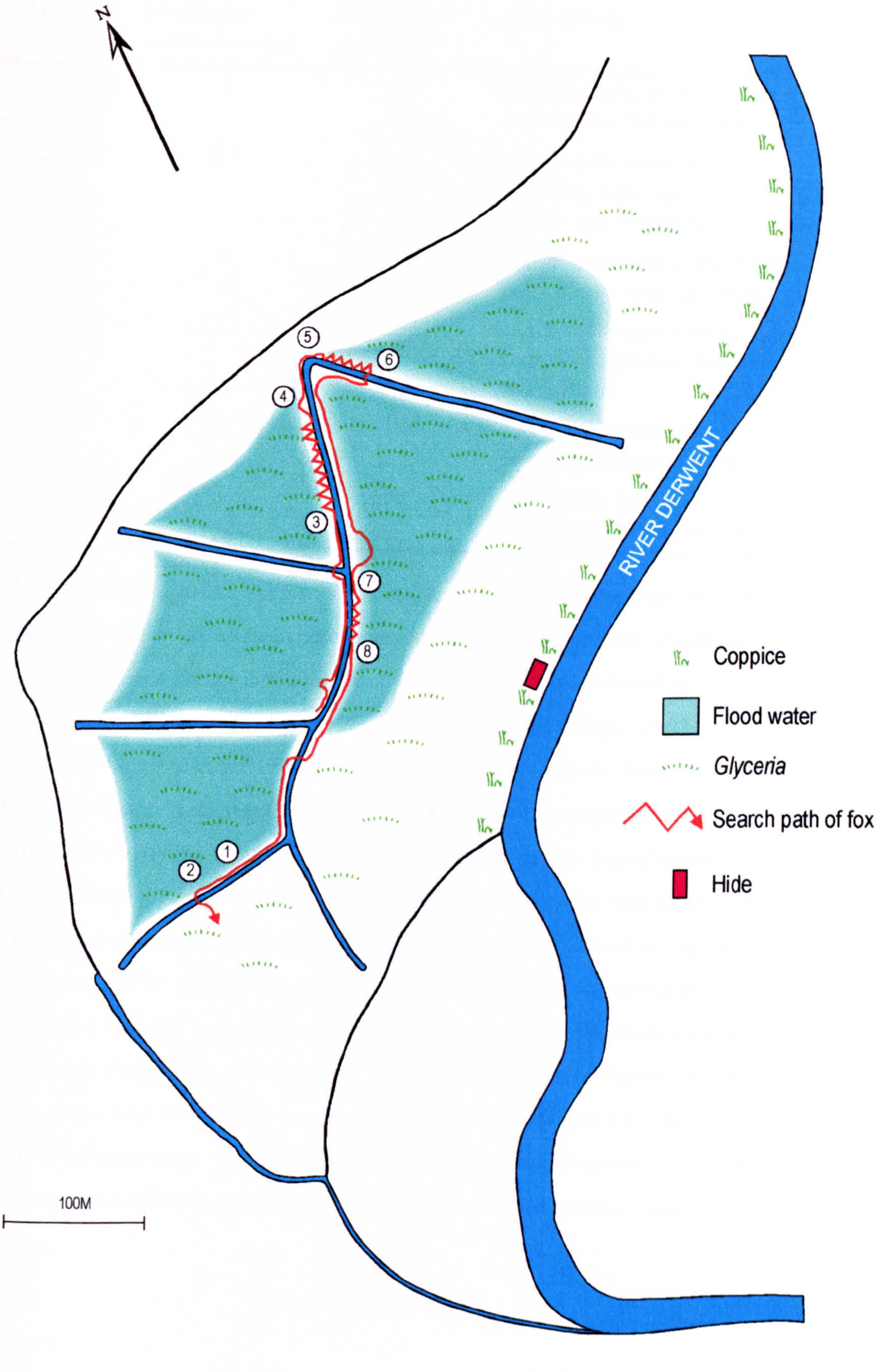
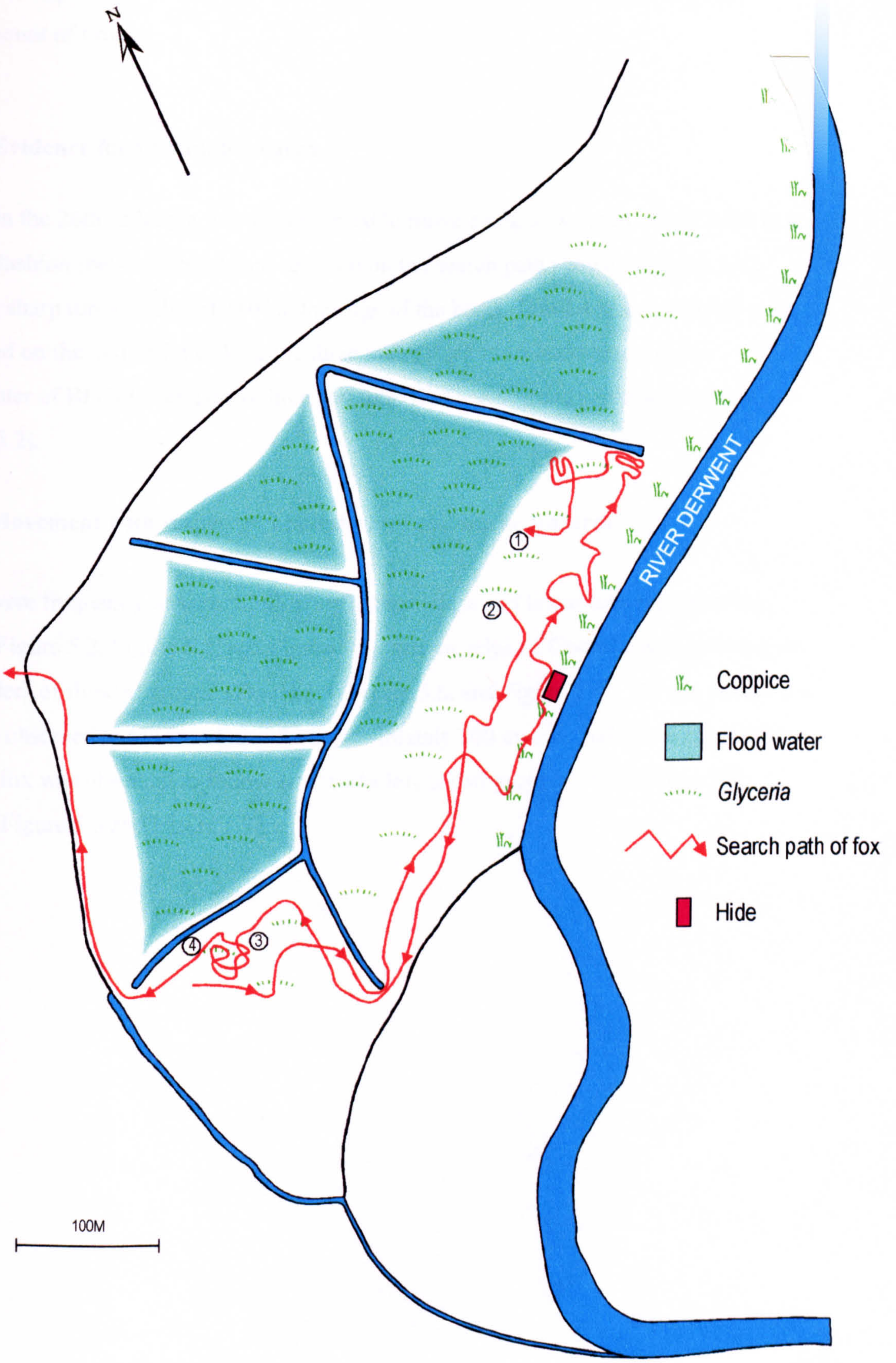


Table 5.3 Site restricted search behaviour in lapwing nesting habitats

Site	Date	Maximum search area (ha)	Duration of search (s)	Bird activity
TI	27 April	1	436	Alarm calling from incubating lapwing for 240 seconds.
BI	2 June	2.5	889	Alarm calls from two pairs of brooding lapwings, and curlew and redshank.
WI	7 June	4	270	Alarm calls from at least two pairs of brooding lapwings.
BI	8 June	3	523	Alarm calls from curlew, and sounds of agitation from coot and mallard.
BI	8 June	0.5	104	Alarm calls from at least 1 pair of brooding lapwings.
NDA	16 June	6	600 +	Alarm calls from at least 5 pairs of incubating lapwings.

At BI on the 8th of June two examples of site restricted search were observed. Between points one and two on the fox's search path (Figure 5.3) the fox moved out of sight as it entered the *Glyceria* beds occupying the centre of the site. The fox remained unseen in the tall vegetation for 523 seconds, during which time it flushed a curlew, which gave vigorous alarm calls for just under 17 minutes, and elicited distress calls from coots *Fulica atra* and mallards which suggest that the fox was actually foraging rather than resting whilst obscured by the vegetation. On the same night, the fox was observed to spend at least 104 seconds in an area of less than half a hectare moving very slowly and turning frequently, between points three and four on the search path shown in Figure 5.3. This area was occupied by a pair of lapwings with a brood of chicks (observed daily in the same area), and the adult lapwings mobbed the fox and gave sixteen alarm calls whilst the fox remained in the vicinity of their brood. At NDA on the 16th of June a fox was seen to enter a sugar beet field of just over six hectares in which at least five pairs of lapwing were incubating eggs. The fox was soon lost from sight as it moved beyond the range of the night vision scope, however, the alarm calls made by adult lapwings

Figure 5.3 The search path of a fox at BI on the 8th of June



(219 individual alarm calls were counted during this period) continued for at least ten minutes, suggesting that the fox remained in the vicinity of the lapwing's nests for at least that amount of time.

5.3.2 Evidence for systematic search

At BI on the 26th of May a fox was observed to move along a two metre wide bund in a zigzag fashion (between points one and two on the search path shown in Figure 5.4), making sharp turns of almost 180° at the edge of the bund. Similar search patterns were observed on the 2nd of June along the three metre wide main bund crossing the floodwater of BI (between points three and four, five and six, and seven and eight in Figure 5.2).

5.3.3 Movement with respect to habitat edges and linear features

Foxes were frequently observed following habitat edges and linear features including bunds (Figure 5.2, Figure 5.4, and Figure 5.5), and the edge of *Glyceria* beds growing on the borders of flooded ground (Figure 5.4, Figure 5.6, and Figure 5.8). On one occasion a fox was observed to follow a fence for approximately 200 metres, and on two occasions at WI a fox was observed to follow tyre tracks left in soft ground for more than 200 metres (Figure 5.6 and Figure 5.7).

Figure 5.4 The search path of a fox at BI on the 26th May.

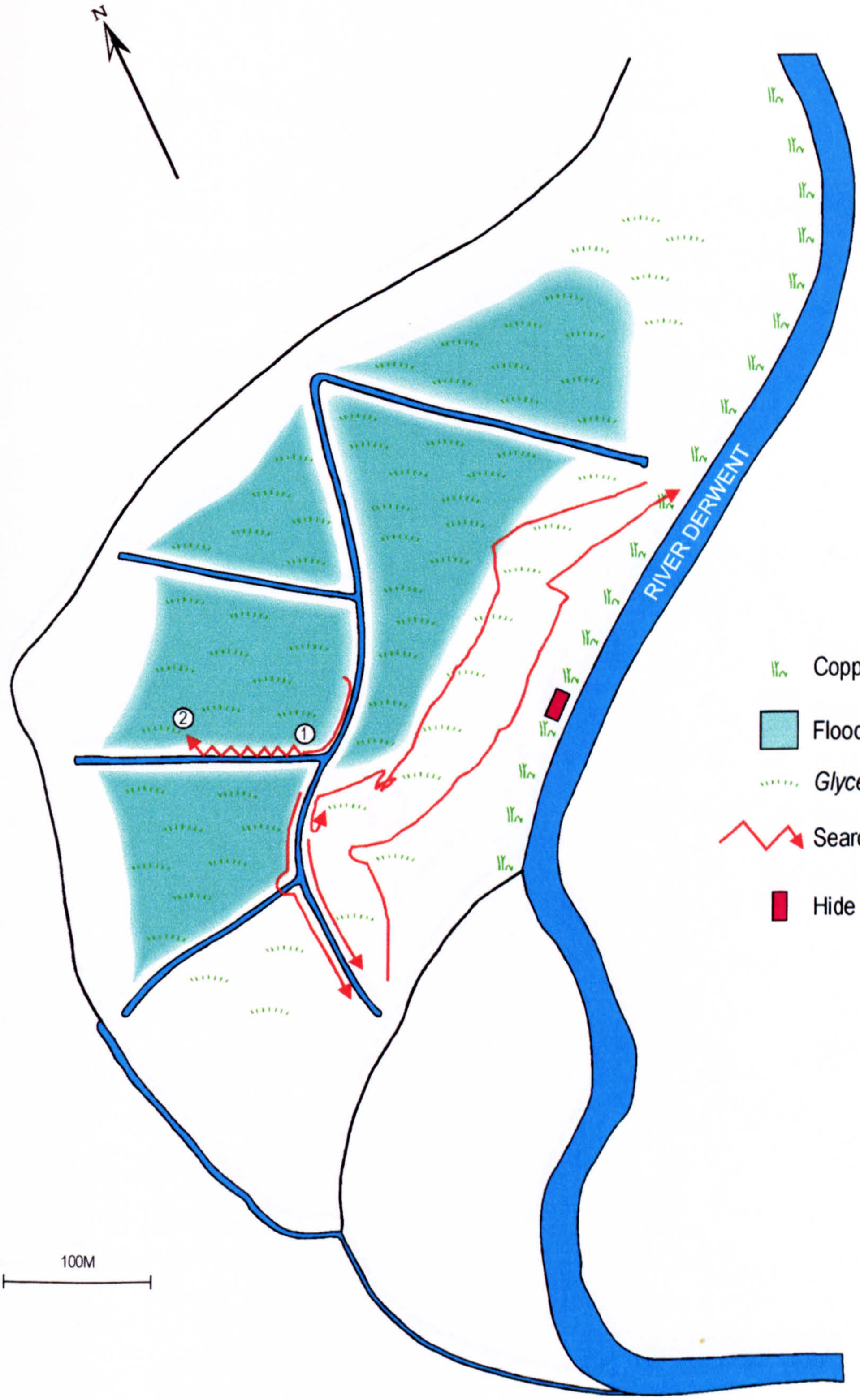


Figure 5.5 The search path of a fox at BI on the 28th of May.

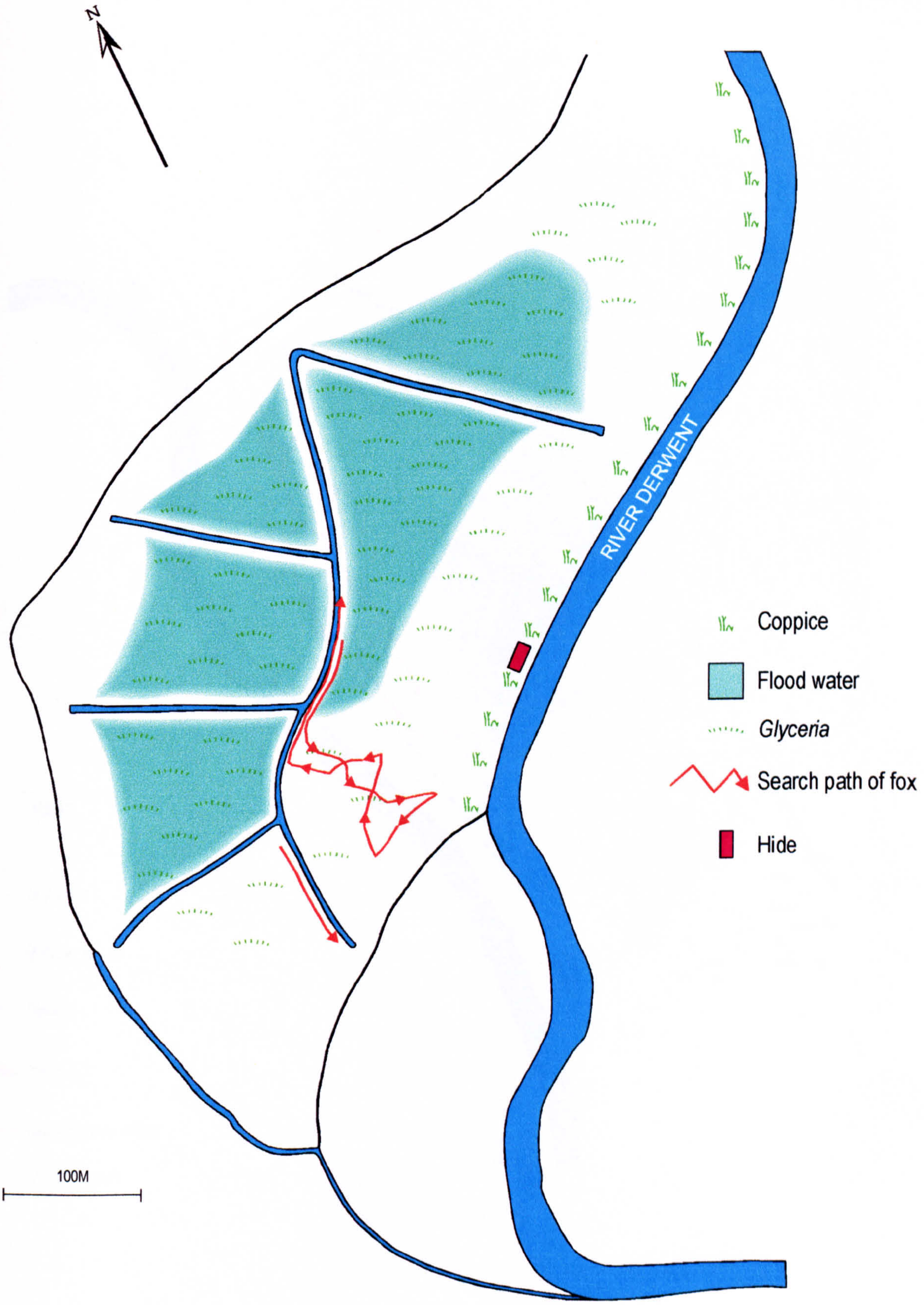


Figure 5.6 The search path of a fox at WI on the 9th of June.

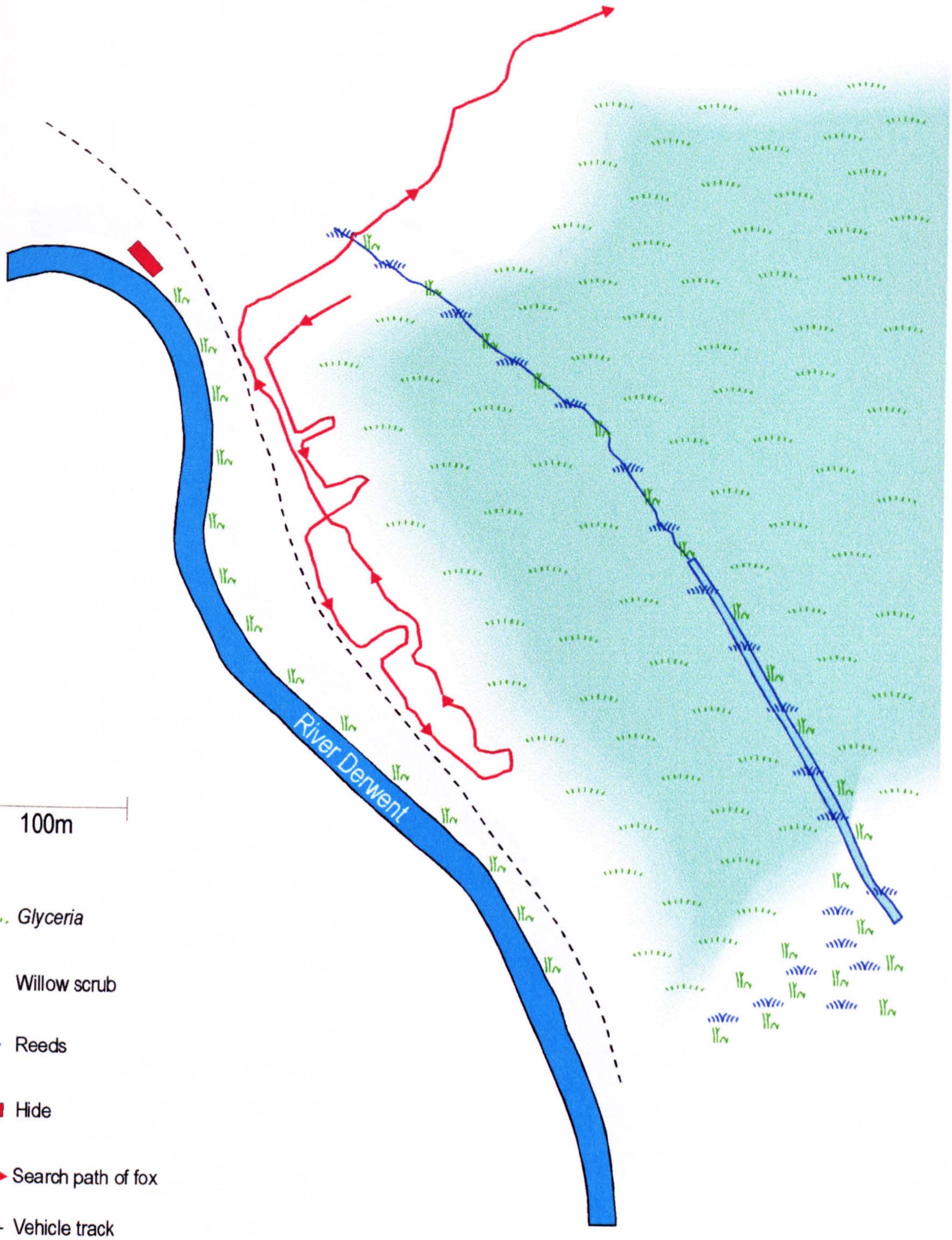


Figure 5.7 The search path of a fox at WI on the 7th of June.

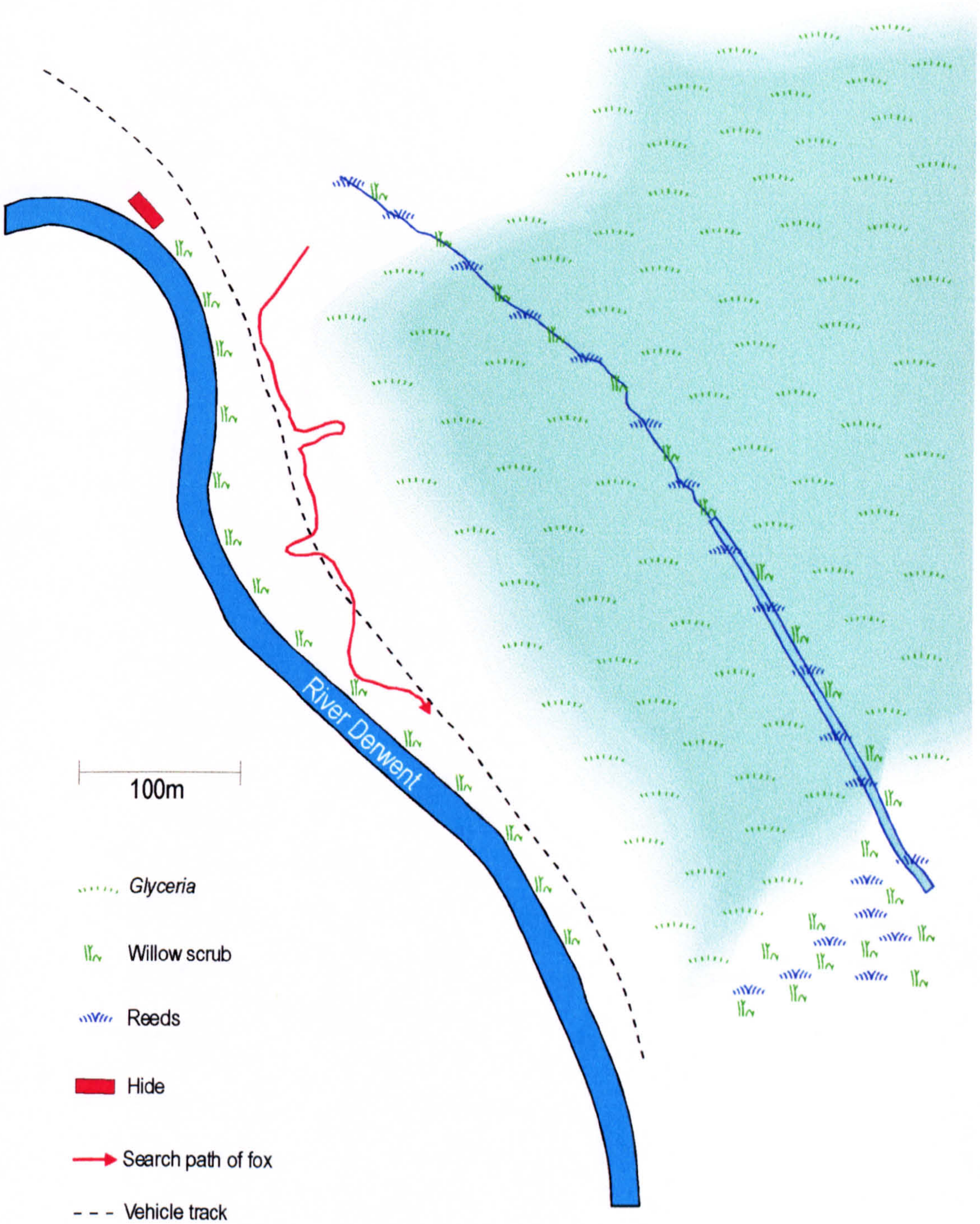
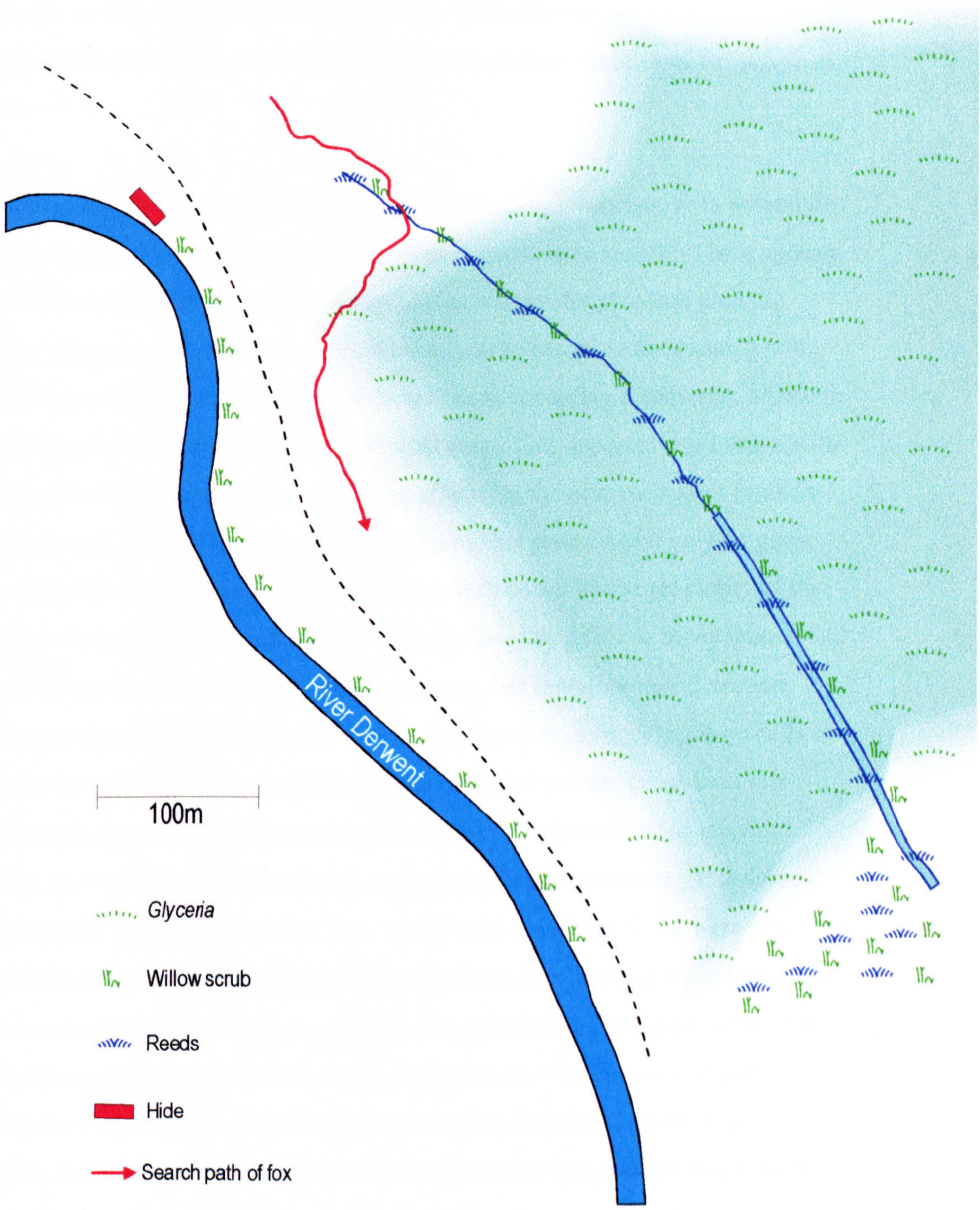


Figure 5.8 The search path of a fox at WI on the 19th of May.



5.4 Discussion

This study provides the first record of the nocturnal activity of foxes in wader nesting sites. Although weather and site specific conditions limited the range and clarity of observations, it was possible to describe some of the important qualities of fox search behaviour.

One particular quality of fox search behaviour in wader nesting habitats, with potentially important consequences for nest predation rate, was site restricted search. There appears to be site restricted search at two scales: foxes initiate a convoluted search path in response to an unknown cue, and secondly, foxes appear to associate their search with particular habitats including bunds and the *Glyceria* beds bordering floodwater, although this cannot be confirmed statistically due to limited data. This apparent association with bunds and floodwater edges may have important effects on the nest success of birds in these linear habitats. Indeed, Kristiansen (1998) found that predation of greylag goose *Anser anser* nests by foxes in reedbeds was strongly influenced by the proximity of the nests to paths in the reedbeds, which were presumably used by foxes as travel lanes. Site restricted search was never preceded by nest encounter, and therefore nest detection cannot have been a necessary cue to initiate convoluted search paths. The alarm calls by adult lapwings are a potential cue for initiating site restricted search. On at least one occasion, however, foxes initiated convoluted search paths before the adult lapwings started calling, and on eight occasions foxes maintained direct movement paths despite vigorous alarm calls by lapwings (Table 5.2). On several occasions, foxes were observed to walk back and forth three or four times over a particular spot in the grass, a behaviour lasting no more than 20 seconds. The examples of convoluted search paths reported in Table 5.3 lasted considerably longer than these examples of short convoluted paths, perhaps because of the presence of stronger or more persistent stimuli from potential prey. Lapwing chicks make loud peeping calls, and although they usually stop calling when adult birds start to alarm call, I have observed that one or more chicks in a brood may continue to call loud enough for me to locate them despite the alarm calls of the

adult birds and the cryptic coloration of the chicks themselves. Lapwing chick calls may serve as cues to initiate site restricted search in foxes.

The sharp zigzag search patterns along bunds, occasionally observed by a fox at one of the study sites is an example of systematic search, because almost all the ground along the three metre wide bund could have be scanned using this search path. Although late flooding prevented any birds nesting on the bund in 1998, it was used by many birds as a roost site. In 1997 at least five lapwing nests, three coot nests, one Canada goose *Branta canadensis* nest and one mute swan *Cygnus olor* nest were situated on this main bund, and all except the mute swan nest were robbed by foxes as revealed by the presence of fox tracks in the vicinity of raided nests (see Chapter 3). This sort of search may have very important consequences for the nest survival of bird species that nest on bunds or other thin strips of habitat. Many ground-nesting species nest in thin strips of habitat including grey partridges and pheasants, which nest on field margins and hedgerows, ducks and geese nesting in the vegetation bordering lakes or floodwater and on bunds, and waders such as snowy plovers that nest on shingle beaches, often close to the debris along the high tide mark.

In the next chapter, a simulation model is presented and used to explore the consequence of reducing the size of nesting habitat fragments on ground-nest predation rate by foxes. The parameters and assumptions of the simulation model are based on the properties of fox search paths shown in this chapter.

6. The influence of search areas on ground nest predation by foxes: a theoretical analysis

Summary

1. A computer model that simulates the search behaviour of red foxes is presented and used to explore the effects of search area on the predation rate of a sessile prey type such as birds nests.

2. Foxes were assumed to forage in a series of straight line movements separated by pauses and turns. Move lengths, pause duration and turn angles were estimated from field observations. The movement and nest encounter processes were assumed to be stochastic in nature. Foxes were assumed to be able to restrict their search to the nesting habitat by recognising habitat boundaries. Five search algorithms were used to simulate different search tactics, including site restricted search in response to nest proximity and systematic search.

3. In linear habitats (≤ 10 metres wide) foxes were assumed to forage in a systematic fashion using a unidirectional zigzag search path.

4. Increasing search area reduces nest predation rate for all models of search behaviour in both linear and broad habitats. In broad habitats, predation rate was particularly sensitive to changes in area from 1 to 4 hectares. In linear habitats, both length and width of habitat had large effects on nest predation rate. In short linear habitats (1- 2 km), nest predation was very high for all habitat widths when total search effort throughout the incubation period was high (> 5 hours). For total search efforts of less than 5 hours increasing habitat width reduced the rate of nest predation considerably. In longer linear habitats (> 4 km), increasing the habitat width had a greater influence on nest predation rates with greater fox search effort (> 5 hours).

5. Evidence to support these results and the implications for predation management are discussed. Finally, a field study to test the predictions of the model is suggested.

6.1 Introduction

The nesting habitats of many ground nesting bird species in Britain have reduced in area due to changes in agricultural practices. For example, in Wales suitable nesting habitats for a range of ground-nesting birds including red grouse, grey partridge, golden plover, lapwings, snipe and curlew, have declined dramatically over the last few decades due to factors such as drainage and improvement of grasslands, and aforestation of uplands (Lovegrove *et al.*, 1995). It has been suggested that fragmentation and the reduction in area of suitable nesting habitat have exacerbated nest predation by mammals, because small habitat patches can be searched more thoroughly by predators than large ones (Potts, 1980; Larivière & Messier, 1998). Many ground nesting bird species have evolved strategies to reduce the risk of nest predation by mammals, including placement of nests in sites inaccessible to predators (Schmidt, 1999), concealment of nest sites (Schiek & Hannon, 1993), cryptic colouration of eggs and spacing out of nests (Tinbergen *et al.*, 1967; Taylor, 1976; Hogstad, 1995). The anti-predator effect of nest concealment and spacing out may be diminished if the nests are restricted to small patches of habitat, particularly if the predator is able to carry out systematic searches of the nesting habitat. The nocturnal observations reported in chapter 4 suggest that foxes are indeed capable of systematic searches, in some habitats at least.

It is impractical to investigate the effect of nesting habitat area on nest predation by foxes in the field. Problems include the difficulty in identifying the predators responsible for nest loss, the small number of suitable study sites, and the difficulty in controlling for other factors such as the distribution and abundance of alternative prey, and the number and breeding status of foxes in the vicinity. In view of these difficulties, it was decided to use a modelling approach to explore the potential effects of a reduction in nesting habitat area on nest predation rate by foxes.

Siniff and Jessen (1969) simulated the movement of red foxes by sampling straight line distances and relative turn angles from probability distributions based on radio telemetry

data. White and Harris (1994) have used similar simulation models, also based on fox radio telemetry data, to determine the expected encounter rates between randomly moving foxes. The simulation model presented in this study generates movement patterns by randomly sampling straight line distances, relative turn angles and pause durations from probability distributions constructed from data obtained during the nocturnal field observations reported in chapters 4 and 5. Several different simulation models incorporating different assumptions on movement behaviour, were set up in order to determine how such assumptions influence the generality of the results. Three main types of search tactic was incorporated into the models. The first search tactic used was slow random search with no response to proximity of prey. The second search tactic was site restricted search in response to either cues originating from the vicinity of lapwing nests (e.g. alarm calling adults), or b) cues originating from other randomly positioned locations corresponding to other prey types such as small mammals. The third search tactic was systematic search in linear habitats using a zigzag search path.

6.2 Method

6.2.1 Model structure

For simplicity, the nesting habitat was represented as a two-dimensional rectangular area. Co-ordinates that represent nest locations were selected at random using a separate program written specifically for this task. In order to mimic the distribution of lapwing nests, the minimum separation distance between nests was assumed to be 15 metres, and the overall density of nests was assumed to be two nests per hectare.

A flow chart showing the model structure is presented in Figure 6.1. The co-ordinates of each nest and the boundaries of the nesting habitat were read into the program from a file at the start of the program. The starting co-ordinates of the fox was randomly chosen from along the nesting habitat boundary in order to remove any bias in nest encounter rate that any single starting position may introduce. Subsequent movements were generated by randomly selecting turn angles and straight line distances from frequency distributions

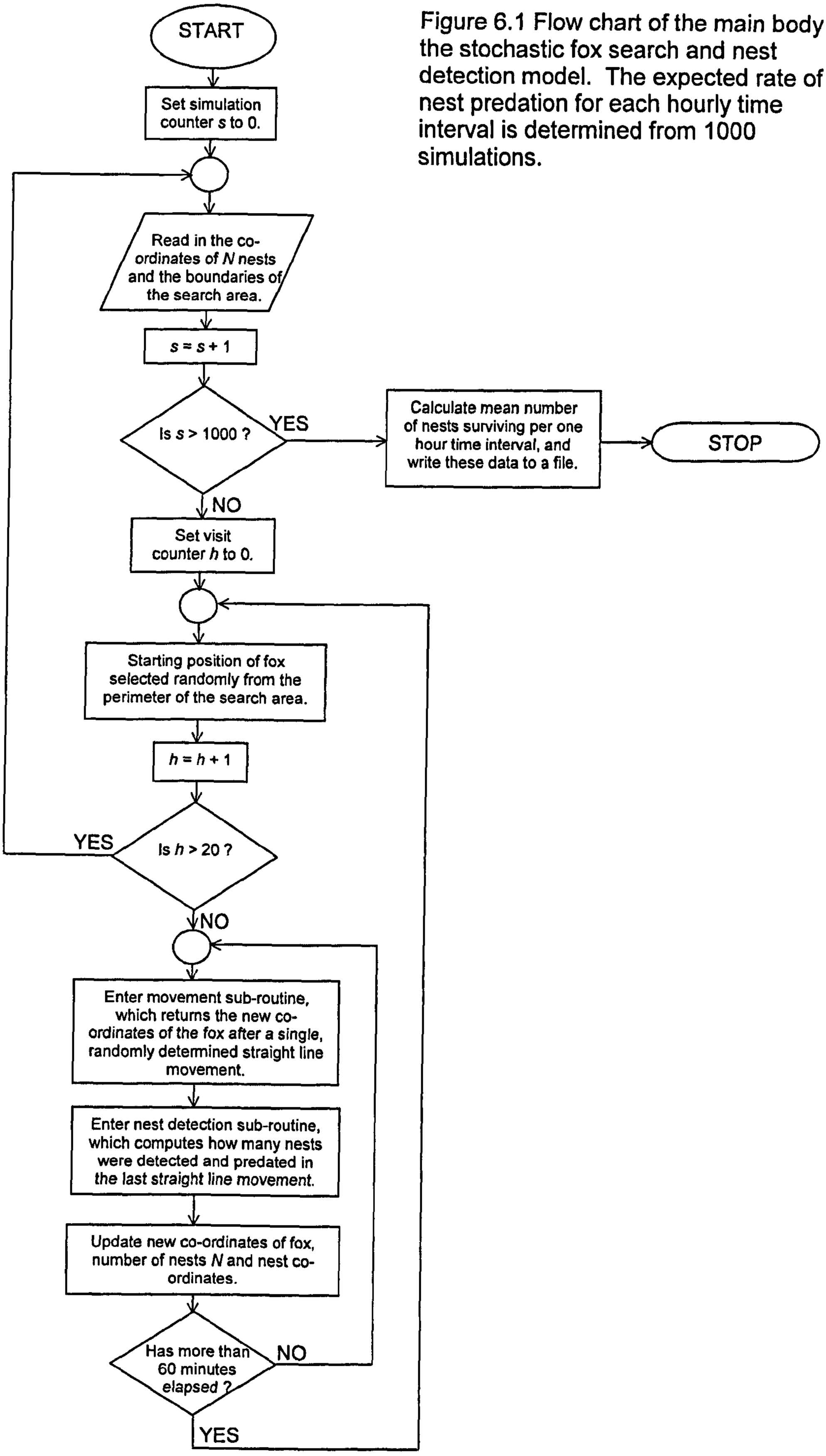


Figure 6.1 Flow chart of the main body of the stochastic fox search and nest detection model. The expected rate of nest predation for each hourly time interval is determined from 1000 simulations.

constructed from data obtained during fox observations. A different sub-routine is used to generate new co-ordinates for each of the different search tactics modelled.

The movement of the fox was assumed to be confined to the limits of the nesting habitat. If the new travel co-ordinated of the fox were outside the boundaries of the rectangular nesting habitat, the same sub-routine will select new travel co-ordinates.

Scanning events were assumed to take place at one second intervals along the line of travel between the old and new co-ordinates. The rationale for this assumption is presented in Section 6.2.3. Nest detection was modelled as a stochastic event, and the probability of detecting a nest increased with proximity. At each one second interval, the distance of the fox to each nest was calculated, and the probability of nest detection was obtained as a function of distance (see Section 6.2.3). A random number generator was used to determine whether or not a nest was detected. If a nest was detected, the nest's co-ordinates were removed from the array in which they were stored, and the fox was assumed to move to the co-ordinates of the nest.

For each model scenario, the fox was assumed to search the nesting habitat for a maximum of twenty hours. The total amount of time spent by a fox in a nesting site over the incubation period will, of course, vary for a number of possible reasons. The maximum amount of time available for searching a site, however, will be constrained by the duration of the incubation period, and the time required by the fox to carry out other necessary activities. Twenty fox hours was arbitrarily chosen as the maximum amount of fox searching effort. Nocturnal observations of foxes carried out in the Lower Derwent Valley showed that foxes spent on average 48.0 seconds foraging in lapwing nesting sites per hour of observation. If it is assumed that there are on average 7 hours per night available for foraging, and that the nesting season is 90 days long, then the estimated total time spent by a fox in a lapwing nesting site would be 8.4 hours. Therefore, the assumption that foxes spend a maximum time of 20 hours searching lapwing nesting sites over the whole breeding season is unlikely to underestimate total search effort.

After each hour of search, the program entered the proportion of nests surviving into an array. Following the convention for Monte Carlo simulations, the model was run a thousand times for each scenario. For each hour of search, the average proportion of nests surviving over the thousand simulations was calculated, and these data were written to an output file.

The program was written in FORTRAN 77 and was run on a Silicon Graphics UNIX mainframe system.

Movement algorithms

Four different movement algorithms corresponding to a selection of plausible fox search tactics were used in the Monte Carlo simulations. Comparing the average predation rates between different search tactics allowed an assessment of the importance of search assumptions on the model's results.

Algorithm 1: This is the simplest of the search algorithms, and is presented as a flow chart in Figure 6.2. From nocturnal observations, the fox was estimated to walk with a velocity of 0.4 metres per second. New co-ordinates were calculated from randomly sampled move lengths and turn angles using simple trigonometry. Move lengths were sampled from a probability distribution of straight line distances moved at walk (Figure 6.3) derived directly from the frequency distribution of move lengths obtained in the field. Turn angles were sampled from a von Mises distribution with a shape parameter c chosen to be equal to unity (Figure 6.4). The von Mises distribution is the circular normal distribution with a mean of zero degrees and left and right hand tails terminating at – 180° and + 180° respectively. The shape parameter c alters the 'sharpness' of the distribution's peak. High values of c increase the height and sharpness of the mean, or in other words, the probability of randomly drawing angles close to zero increases as the value of c is increased. The von Mises distribution was chosen because it reflected the properties of the frequency distribution of turn categories obtained in the field in being symmetrical around

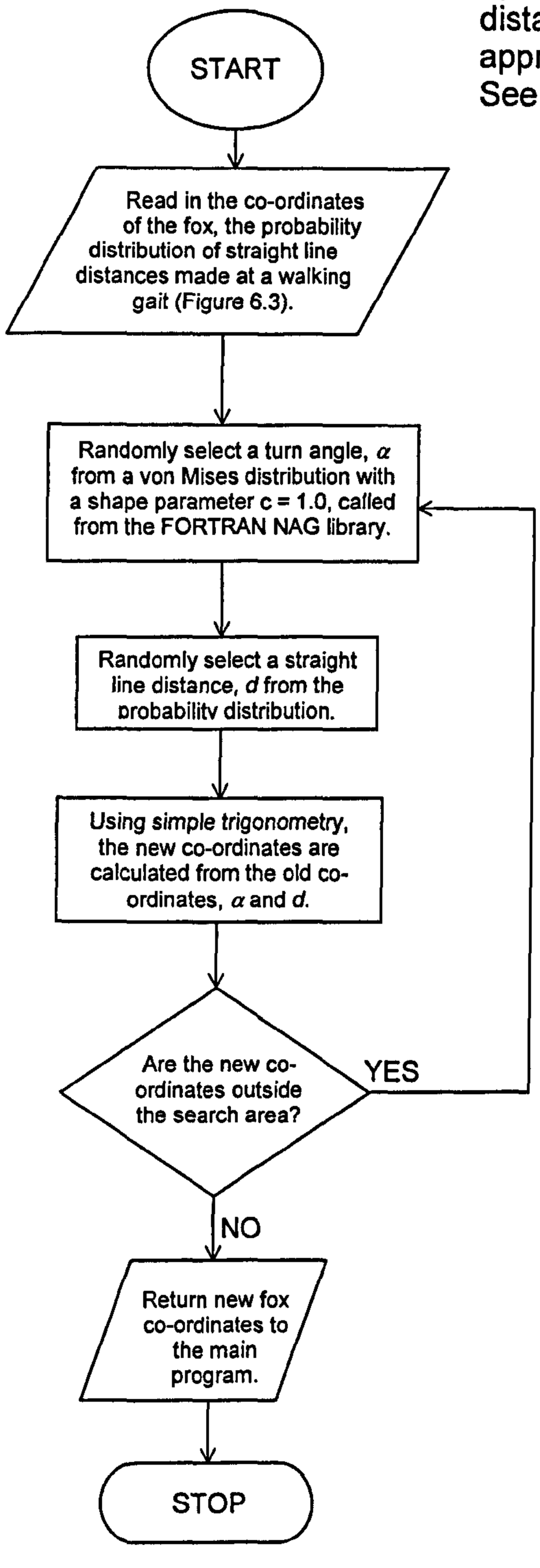


Figure 6.2 A flowchart for search algorithm 1. Movement is modelled by randomly selecting straight line distances and turn angles from appropriate probability distributions. See text for further explanation.

Figure 6.3 Probability distribution of straight line distances moved by foxes at a walking gait constructed from data obtained during nocturnal observations of foxes.

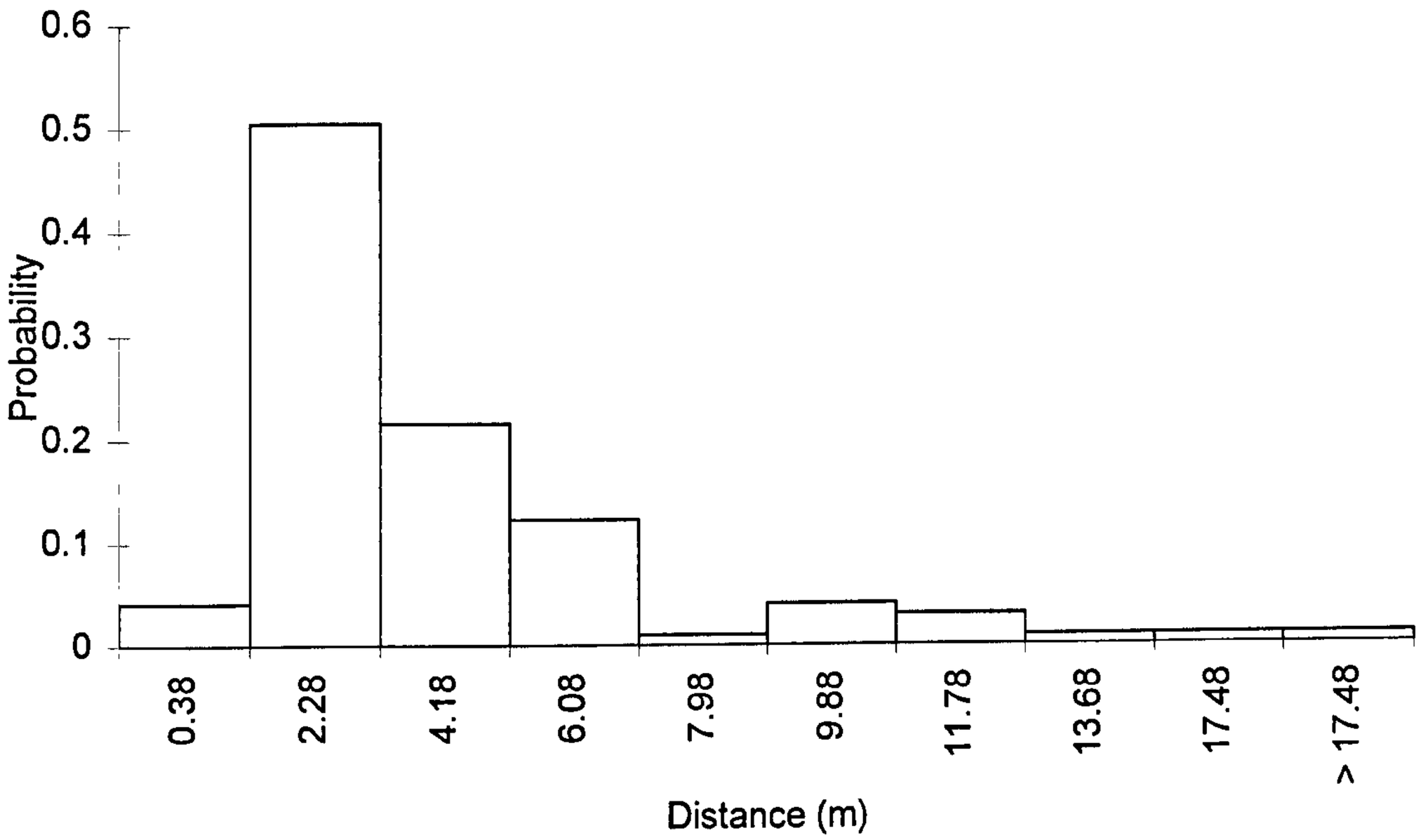
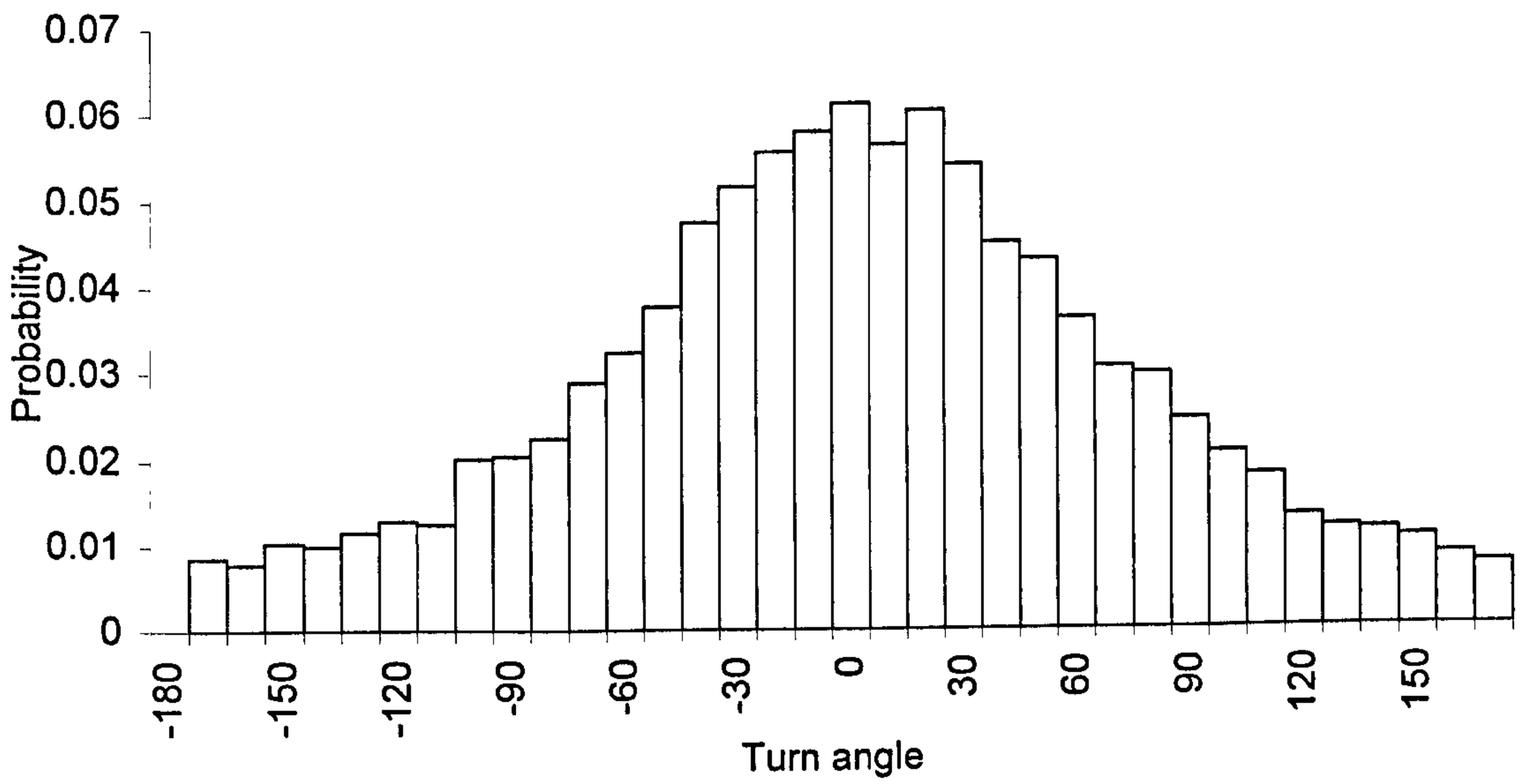
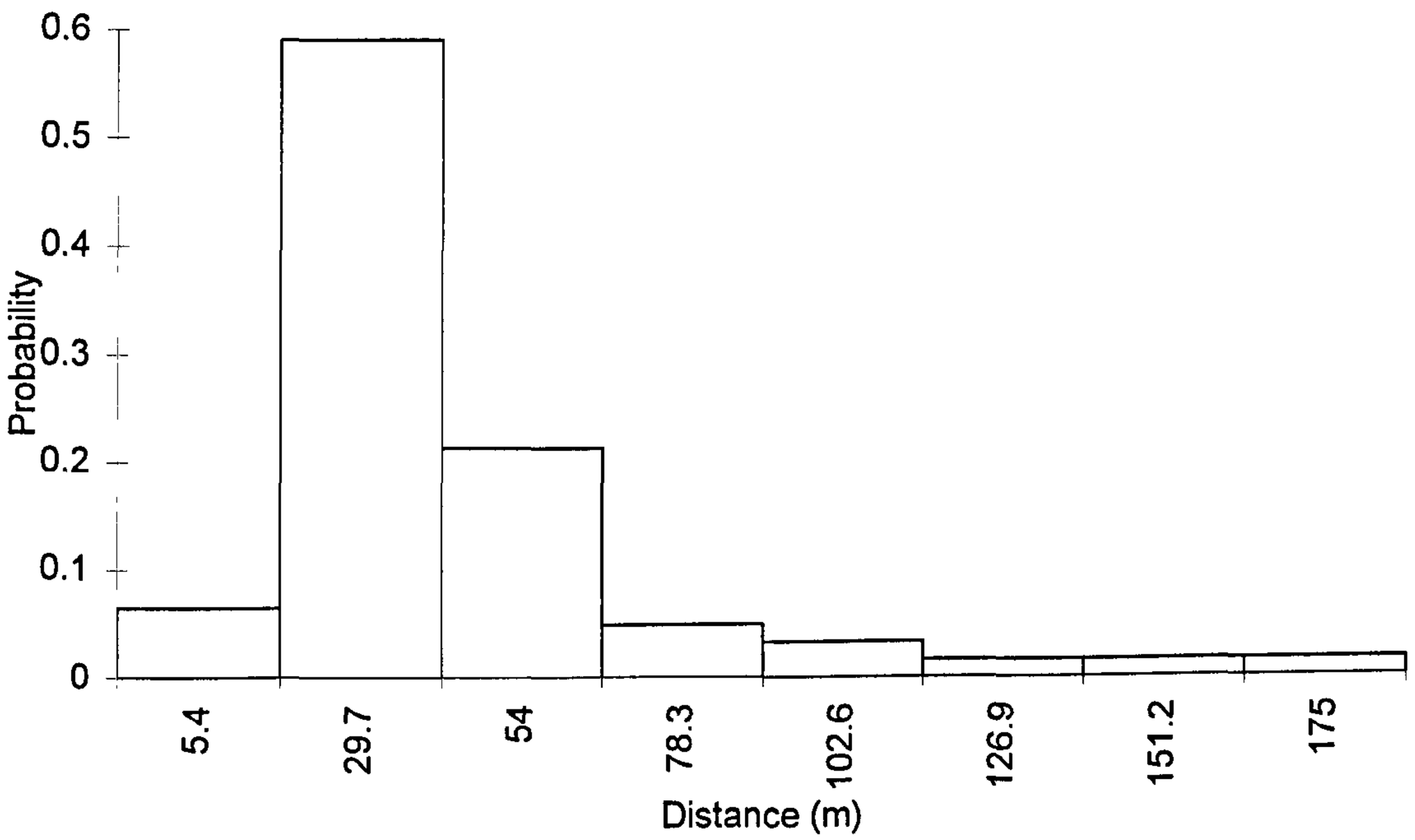


Figure 6.4 Probability distribution of turn angles generated from 10,000 angles randomly sampled from a von Mises distribution with parameter c = 1.0



a mode of zero degrees. shows the frequency distribution of 10,000 angles selected from a von Mises distribution with a shape parameter of one using a commercial sub-program available for FORTRAN 77 (NAG library). In the field observations, turns were categorised into approximately 45 degree sectors and it was not possible to estimate the shape parameter *c* from these data. Consecutive move lengths and turn angles were assumed to be independent.

Figure 6.5 Probability distribution of straight line distances made by foxes at a trotting gait



Algorithm 2: More complexity was introduced into this algorithm in order to reflect important qualities of observed search paths. This search tactic was less likely to underestimate nest predation rates than search tactic described by algorithm 1, which was selected for its simplicity. In this case, foxes were assumed to move in relatively straight search paths until cues from the nest or incubating bird were detected (flow chart presented in Figure 6.6). Similar to nest detection itself, the probability of detecting such cues increased with proximity to a nest. The shape of this function is described in section 6.2.3. If cues from the nest were detected the fox was assumed to adopt a slower more convoluted search path imitating site restricted search. During straight search paths foxes

were assumed to move at either a walk or a trot, as observed in foxes during nocturnal observations. New co-ordinates were obtained using the same method as algorithm 1 except different probability distributions were used. During straight search paths, straight line distances moved at a walk were randomly sampled from the probability distribution shown in Figure 6.3, and straight line distances made when trotting were randomly sampled from a modified version of the probability distribution shown in Figure 6.5. The probability distribution of straight lines made when trotting shown in Figure 6.5 was derived directly from the corresponding frequency distribution constructed from data obtained in the field. However, since the distribution was made from relatively few measured distances ($n = 61$) the distance intervals on the x axis are very large. To use this probability distribution in the model would be to assume that when trotting, foxes make few, widely differing, discrete straight line movements, an assumption that is clearly not true. In the model, straight line distances were divided into more realistic two metre intervals. Within each of the larger intervals shown in Figure 6.5 it was assumed that there was an equal probability of selecting any two metre interval.

Although there was evidence to suggest that subsequent moves made at the same gait were clumped (i.e. autocorrelation in gait), for simplicity it was assumed that consecutive moves were independent. Since foxes were observed to move at a walk more often than at a trot, both in terms of duration and number of moves, a bias was given towards the selection of a walking gait at each move. The most important feature of these direct search paths in terms of their influence on nest predation rate was that they reduced the time spent in areas where there were no nests, so a bias in the selection of gait may be important. However, since nest and 'cue' detection events were assumed to occur once every second, the increase in velocity associated with gait will also reduce the probability of detecting a nest. Trotting foxes were estimated to be moving at a velocity of 2.64 metres per second. In the model at least, there is a trade off between reducing the time spent in less productive areas and reducing the risk of missing nests by increasing velocity. Although it is accepted that these last two assumptions (i.e. no autocorrelation in gait, and a 70:30 bias towards a walking gait, based on the ratio of straight line movements made at a walk and a trot) may have some influence on nest predation rate, a comparison of the nest predation rates

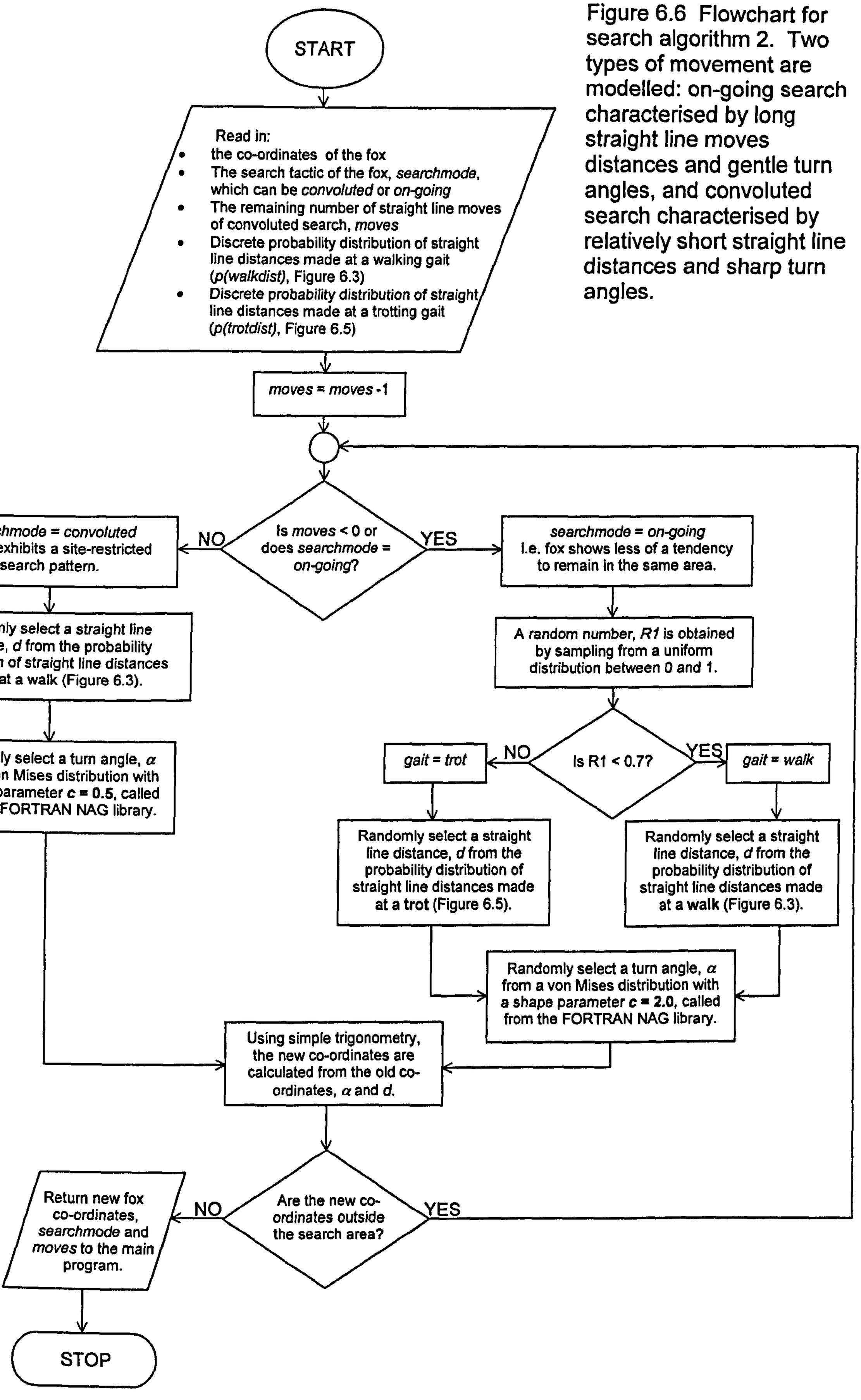
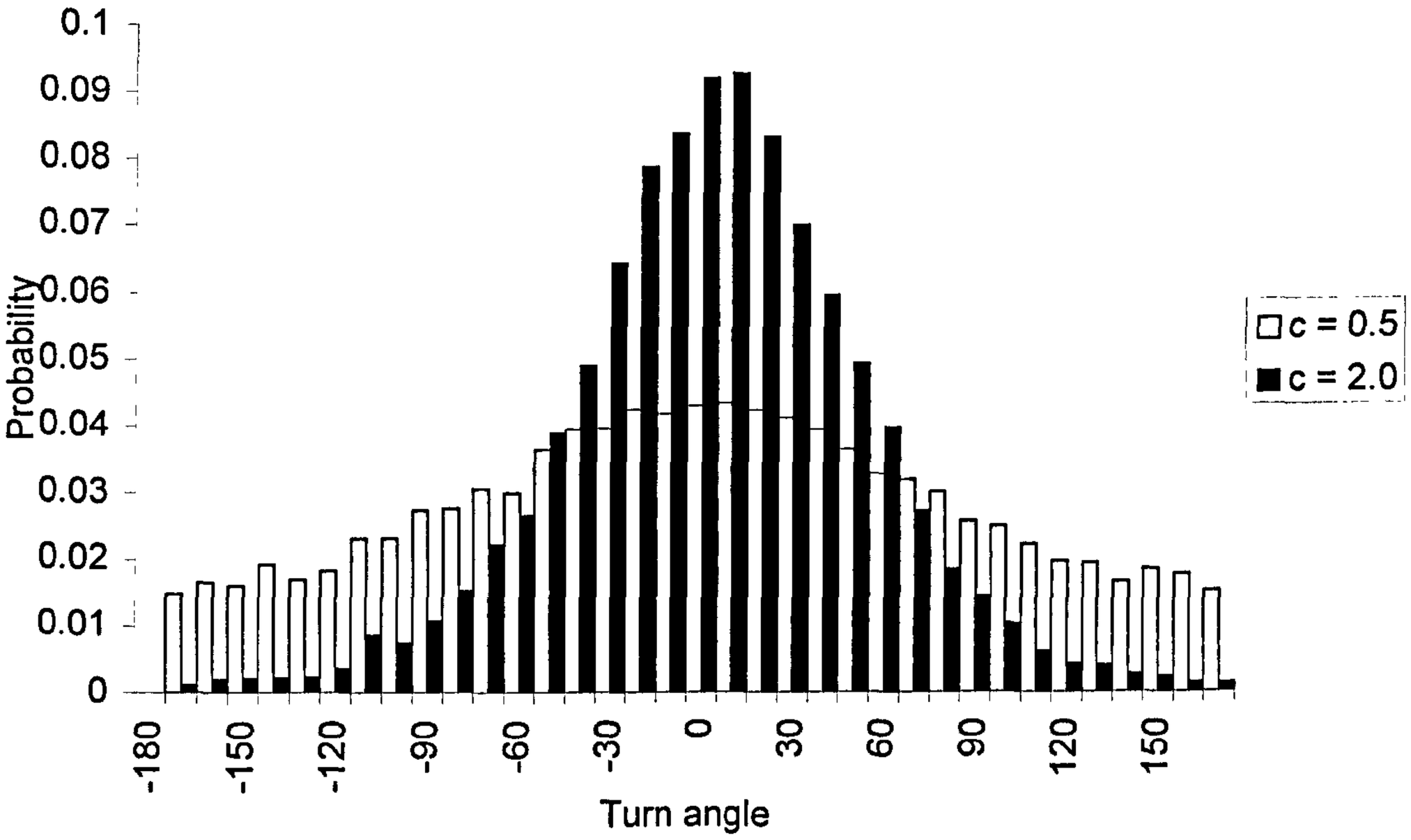


Figure 6.6 Flowchart for search algorithm 2. Two types of movement are modelled: on-going search characterised by long straight line moves distances and gentle turn angles, and convoluted search characterised by relatively short straight line distances and sharp turn angles.

generated from this algorithm with the nest predation rates generated by algorithm 1 should give some idea how much these assumptions could influence the qualitative interpretation of the results. Turn angles for straight search paths were obtained by randomly sampling from a von Mises distribution with a shape parameter $c = 2$, which results in a relatively strong bias for going straight on (Figure 6.7). During convoluted search paths foxes were assumed to move only at a walk (in agreement with field observations) and straight line distances were randomly sampled from the probability distribution shown in Figure 6.3. Turn angles were randomly sampled from a von Mises distribution with a shape parameter $c = 0.5$ which increases the frequency of sharp turns and generates a more convoluted search path (Figure 6.7).

Figure 6.7 Probability distribution of turn angles generated from 10,000 angles randomly sampled from a von Mises distribution with parameter c = 0.5 and 2.0



The number of moves involved in observed convoluted search paths in the vicinity of nests vary as reflected in the range of durations of observed convoluted search paths (Table 5.3). The minimum number of moves triggered by some cue related to the proximity of prey in reality is likely to depend on the nature of the cue, for example, the detection of the sound and smell of a prey animal may elicit longer site restricted search than, say, a rustle in the

grass. For simplicity, in the model it is assumed that each time the fox detects cues, the number of moves of convoluted search is reset to a fixed number, representing the minimum number of moves. In this way, the model fox may increase the duration of convoluted search if it continues to receive cues related to the proximity of prey. The minimum number of moves may be important: too few moves, and the fox risks leaving an area before detecting nearby nests, too many moves, and the fox risks wasting time in an area after the nest itself is detected. In order to assess the importance of the assumed minimum number of moves in convoluted search paths on nest predation rate, two contrasting numbers were used in the model. Convoluted search paths of four to six movements were frequently observed. On the six occasions when foxes carried out site restricted searches apparently in response to the activity of adult lapwings, convoluted search paths were maintained from 104 seconds to more than 600 seconds. However, due to poor viewing conditions it was not possible to count the number of straight line movements made during these events. As a result, convoluted search paths of 10 straight line movements and 50 straight line movements were selected arbitrarily as contrasting site restricted search tactics. If a nest was encountered, site restricted search was assumed to cease.

Algorithm 3: This algorithm was identical to algorithm 2 in most respects, except that the probability of initiating convoluted search paths increased with proximity to randomly chosen co-ordinates representing an alternative prey type. This algorithm simulates the effect of incidental nest predation described in Section 4.1. In order to allow direct comparison with the results from algorithm 2, the density of alternative prey was assumed to be equal to the density of nests. This algorithm was also run with two contrasting minimum number of moves made during convoluted search (i.e. 10 and 50 moves).

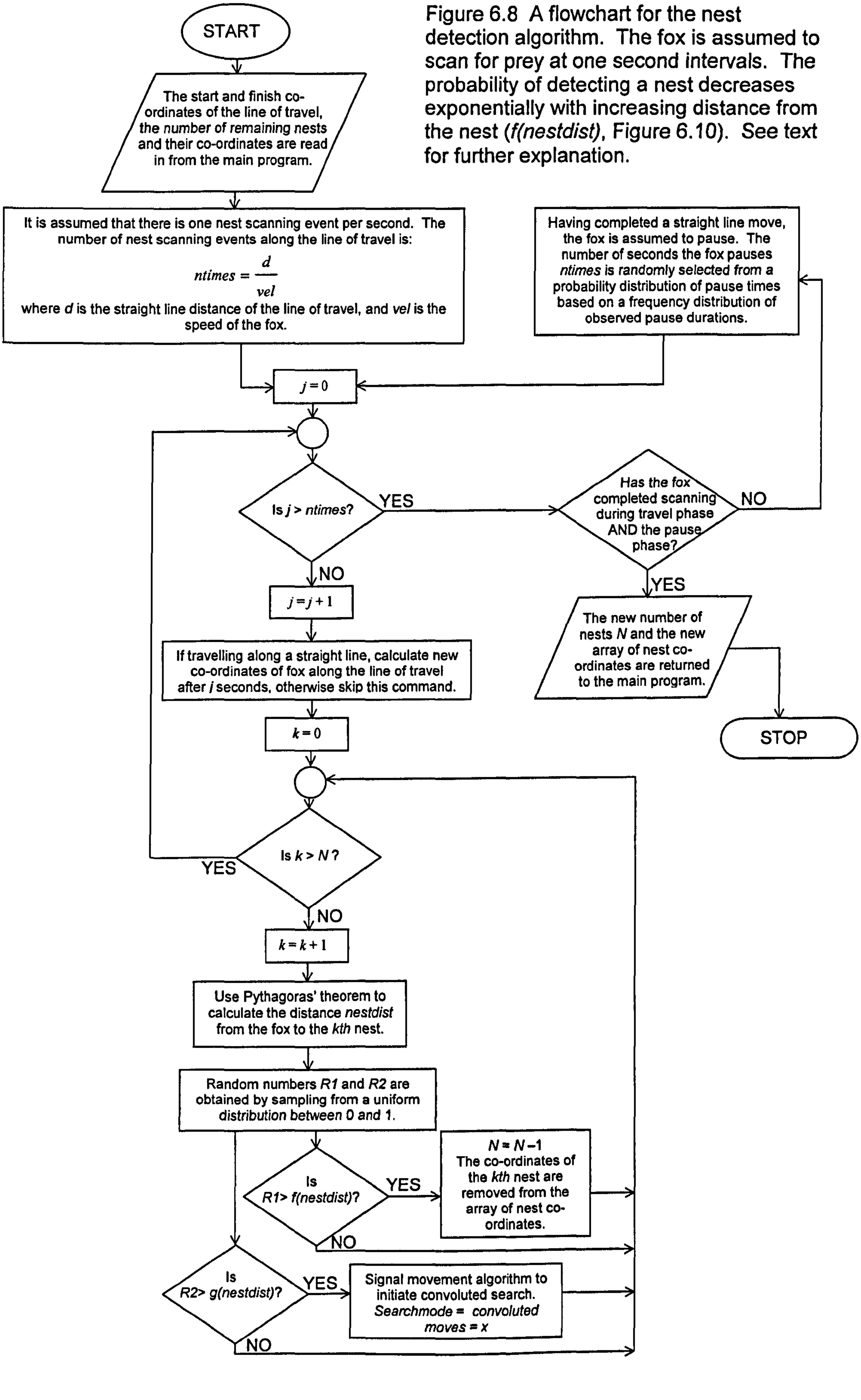
Algorithm 4: An interesting quality of fox search behaviour observed during nocturnal observations was zigzag movement along a linear habitat suggesting systematic search. This final algorithm mimics zigzag search paths along linear habitats. The linear habitats were assumed to be elongated quadrilaterals lying along an x axis. Zigzag search was modelled by confining the movement of the fox to consecutive hypothetical blocks along

the linear habitat. To achieve a zigzag pattern, the direction of movement was reversed in each consecutive block. For each move within blocks, the new *y* co-ordinate was obtained by subtracting or adding (depending on movement direction) a randomly sampled distance from the probability distribution shown in Figure 6.3 to the old *y* co-ordinate. The new *x* co-ordinate was obtained by randomly sampling from a uniform distribution between the lower and upper *x* co-ordinates of the current block. Clearly, the width of the block can alter how thoroughly the habitat was searched: thin blocks can give rise to more thorough search patterns than wide blocks. A number of search paths can give rise to systematic search, including parallel sweeps which is approximated by a zigzag search path. The distance between parallel sweeps in a systematic search should be twice the maximum detection distance to the target (Bell, 1991). The maximum possible nest detection distance assumed in this model was just over three metres, although the probability of detecting nests at that distance was very low (see section 6.2.3). The choice of the width of blocks will influence the average distance between parallel sweeps, and may be an important factor determining nest predation rates. For this reason, this algorithm was run with two contrasting block widths: six metres and four metres. These figures for block width were chosen because the average distance they produce between consecutive sweeps were within the maximum nest detection distance. The zigzag search paths made by foxes during nocturnal observations involved very sharp turns (close to 180° in many cases) which would have produced short distances between consecutive sweeps and a thorough coverage of the area. It was assumed that the fox would continue to search from the beginning of the linear habitat after coming to the end of the habitat until the maximum search time of twenty hours had elapsed.

6.2.2 Nest detection

The stop-start nature of observed fox movement whilst searching in nesting habitats suggests a saltatory (movement followed by a pause) search mechanism. The model assumed that foxes scan for prey once every second either when moving or when stationary during pauses. At the end of each straight line distance moved, the model

Figure 6.8 A flowchart for the nest detection algorithm. The fox is assumed to scan for prey at one second intervals. The probability of detecting a nest decreases exponentially with increasing distance from the nest (*f(nestdist)*, Figure 6.10). See text for further explanation.



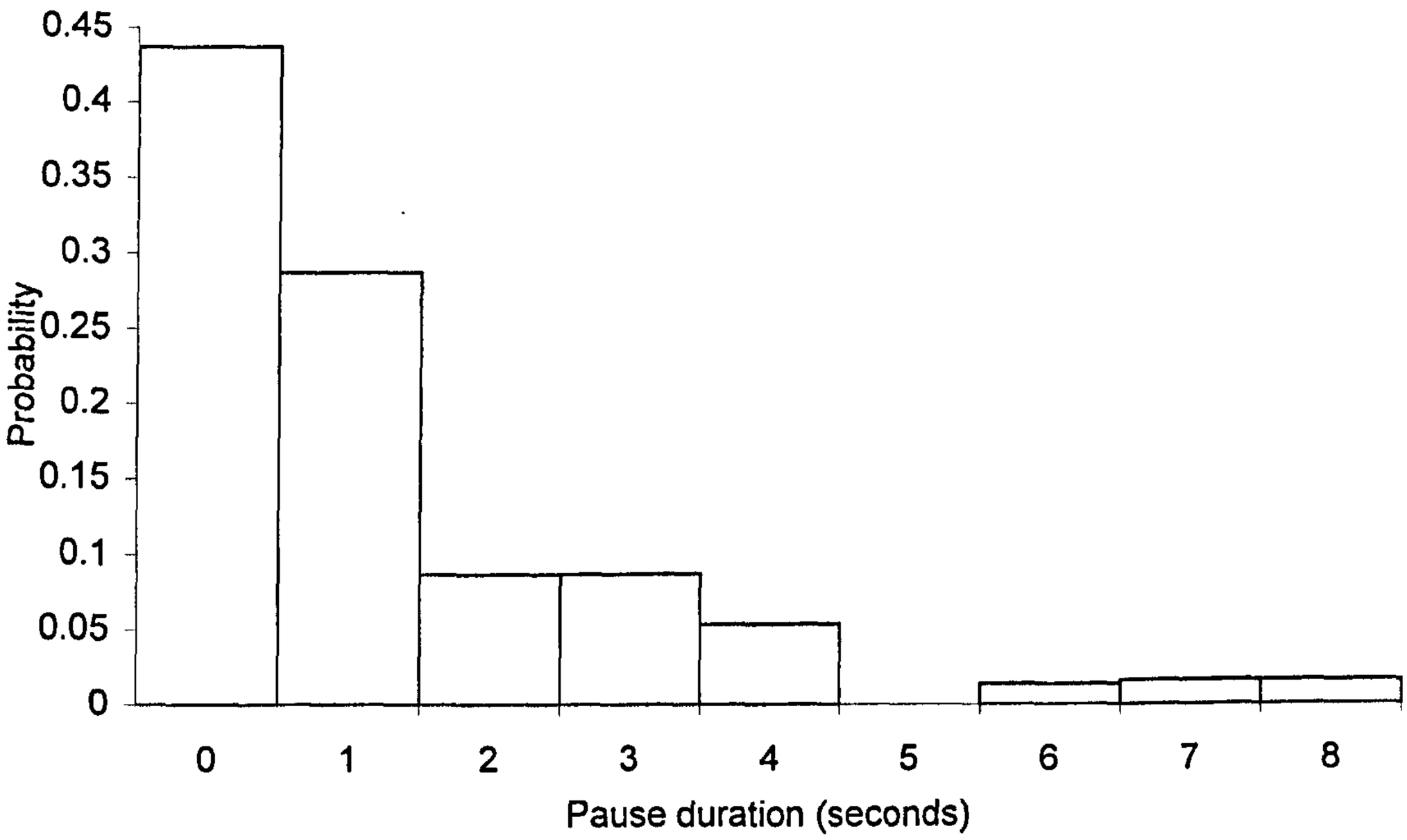
randomly selected a pause duration from the probability distribution shown in Figure 6.9. This probability distribution was derived directly from the frequency distribution of pause durations obtained from nocturnal observations (n = 140).

Low intensity sounds made by prey may be obscured by the noise created by a fox moving through vegetation. When foxes are moving faster, they are likely to create more noise and be less likely to detect prey. By assuming scanning events occur at regular time intervals rather than distance intervals, the overall probability of nest detection will tend to be lower at greater speeds, thus incorporating a potentially important quality of prey detection. Although the choice of one scan per second is arbitrary, it does not lead to unrealistic nest predation rates. Most waders have cryptic nests and well camouflaged eggs in open ground, and many species of ducks and game birds have nests that are well concealed in vegetation (Cramp & Simmons, 1983), therefore it is unlikely that nocturnal predators such as foxes would be able to detect these nests using vision unless they are very close. Like other canids, foxes have an acute sense of smell, however, Hudson (1992) noted that trained pointing dogs were unable to detect incubating red grouse from distances greater than 0.5 metres suggesting that scent emissions are very low, and Byrkjedal (1987) found that pointing dogs were successful at finding golden plover nests with incubating birds but not dotterel nests. In the last example it was noted that the gun-dog was unable to find the unattended nests of either species, suggesting that scent emissions came from the incubating adult rather than the nest and eggs. This may be very important to vigilant ground-nesting birds such as lapwings and other wader species that quit the nest when they have detected a ground predator that is still a long distance away (Cramp & Simmons, 1983; Byrkjedal, 1987). There is likely to have been a strong selection pressure for nests that are exposed to predators to be inconspicuous, and so the maximum detection distance of cryptic nests by foxes is not likely to be more than a few metres.

In the simulation model a negative exponential curve was used to describe the probability of nest detection with increasing distance from the fox (Figure 6.10). A negative exponential was chosen because both the intensity of sound and the concentration of odour

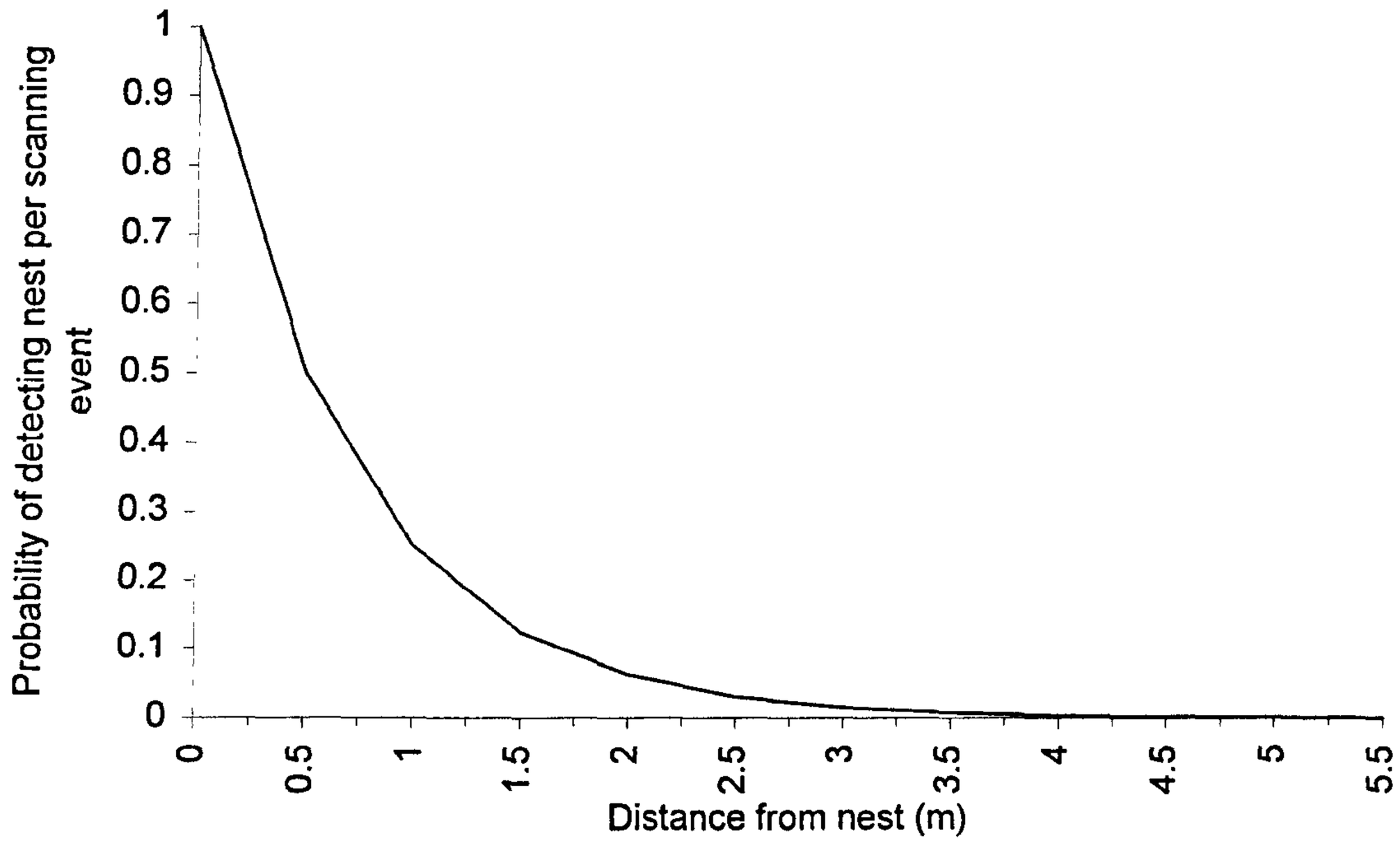
will tend to decline with distance from a point source in this fashion (e.g. Catchpole & Slater, 1995). It was assumed that when the predator is immediately next to a nest it will always detect it, and that this probability declines to almost zero at a distance of 3.5 metres (P(nest detection) = $e^{-1.40.\text{distance}}$). Given the observation of Hudson (1992) and Byrkjedal (1987), these assumptions are unlikely to underestimate the nest detection efficiency of foxes.

Figure 6.9 Probability distribution of pause durations made by foraging foxes, derived from a frequency distribution constructed from data obtained during field observations.



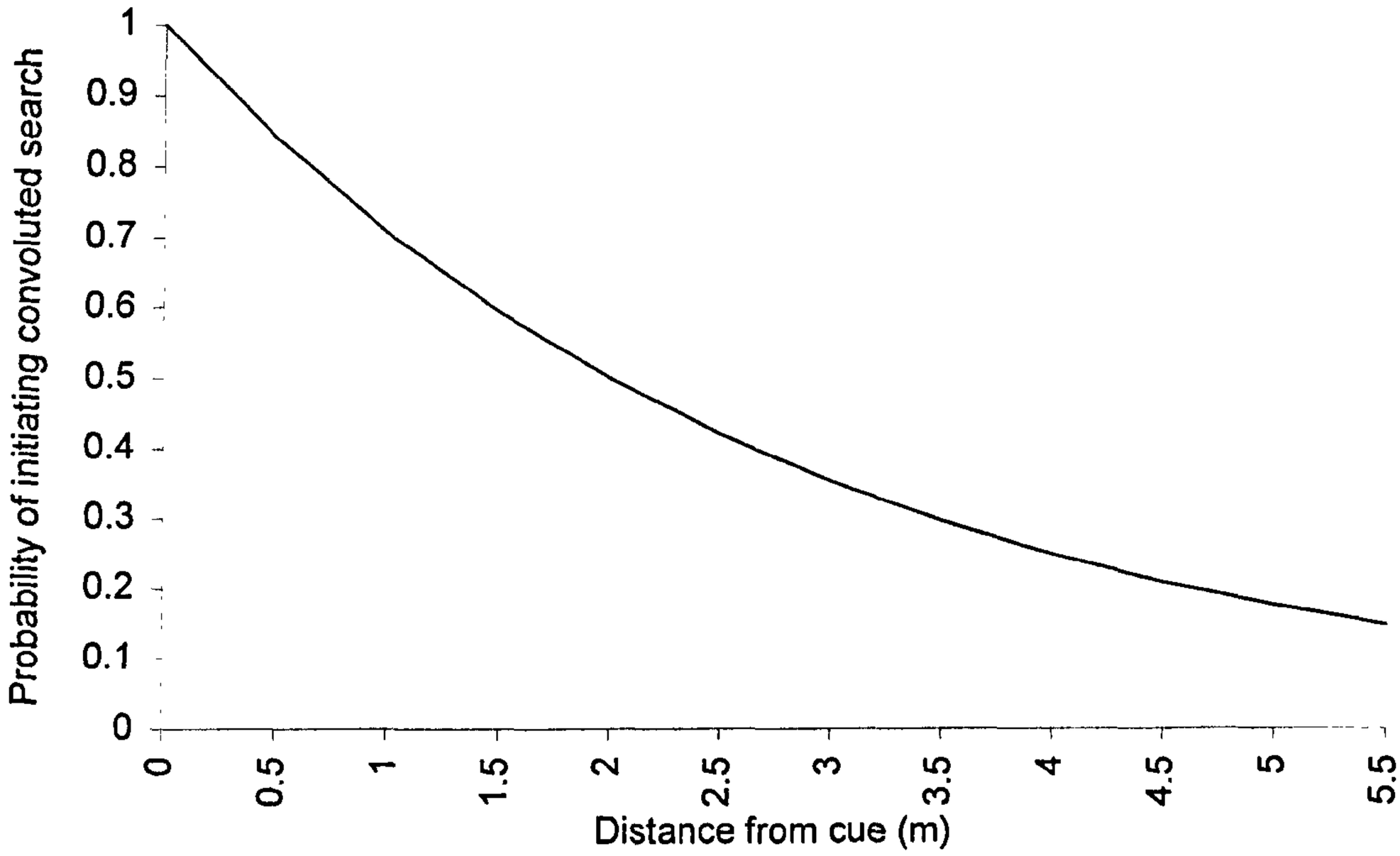
Clearly, the assumptions made about the nest detection capability of foxes will have an important influence on the predation rates predicted by the model. However, the model was not re-run with contrasting nest detection curves for the following reasons: 1) the large number of extra model runs required would dramatically increase the amount of time needed to run and analyse the models and produce an unwieldy amount of data, not all of which is necessarily useful, and 2) the purpose of this modelling exercise is to explore the effects of changing search areas on patterns of predation and not to actually predict nest predation rates themselves.

Figure 6.10 The probability of nest detection against distance from the nest, *f(nesdist)*.



Similar to nest detection, the probability of initiating convoluted search was assumed to decline exponentially with distance from the source of a cue (Figure 6.11). Cues *not* leading to immediate nest detection that may initiate site restricted search include a) observing an adult bird flushed from cover, b) the mobbing and alarm calling behaviour of adult birds, c) scent from the incubating bird or the nest d) the capture of one chick in a brood and e) low intensity sounds from the chicks or hatching eggs. It is known that distraction display behaviour of brooding hen game birds can initiate site restricted search (Sonerud, 1988). Similarly, foxes were shown to initiate site-restricted search in the presence of mobbing adult lapwings (Table 5.3). However, foxes did not always respond to mobbing lapwings by initiating site restricted search (Table 5.2), and the distance at which the adult lapwings responded to a fox was variable, ranging from over 40 metres to less than 10 metres. Searching foxes were shown to elicit significantly longer bouts of mobbing and alarm calling from foxes when more broods were present. The capture of a chick may stimulate a concentrated search for the others in the same brood. The curve presented in Figure 6.7 is described by: (P(initiate site-restricted search) = $e^{-0.35.(\text{distance from cue})}$).

Figure 6.11 Probability of initiating convoluted search with increasing distance from nest or alternative prey, *g(nestdist)*.



This negative exponential curve was arbitrarily chosen, but shows two properties of the distance-dependent probability of initiating site restricted search: 1) the probability of initiating site restricted search near a brood or a nest is greater than the probability of nest detection at any given distance and 2) the probability of initiating site restricted search declines with increasing distance from the source of the cue.

6.2.3 Model Scenarios

For the purpose of this analysis, the nesting habitats of ground-nesting birds are divided into linear and broad habitats. The nesting habitat of many species can usually be recognised as belonging to one or the other of these two categories. For example, grey partridges and pheasant are frequently found nesting in hedgerows or beside fences, and ducks are often found nesting in strips of dense vegetation growing on bunds or along the edge of open water. These habitats are clearly linear or, strictly speaking, curvilinear. Many waders such as lapwings, curlews and redshank nest in grasslands that may be considered as broad habitats, because patches of grassland usually have a relatively low edge to area ratio. The area of both linear and broad nesting habitats vary considerably.

For example, from a survey of ten farms in Britain, Rands (1986b) measured hedgerow densities ranging from 2.7 to 36.6 km per square kilometre of countryside. Other linear habitats may be considerably shorter, for example, there were approximately 1.5 km of bunds per square kilometre at Bank Island in the Lower Derwent Valley study site. In the Lower Derwent Valley distinct nesting sites for various waders consisting of uninterrupted wet grassland varied from just over a single hectare (Thornton Ings) to over 35 hectares (Wheldrake Ings) in area.

For simplicity, it was assumed that broad habitats were square and that the nest density in broad habitats was assumed to be two nests per hectare, a relatively high, but not atypical nest density for lapwings (see chapter 3). The models were run in eight broad habitats of 1, 2, 4, 6, 8, 10 and 12 hectares. The nest density in linear habitats was assumed to be ten nests per kilometre, a realistic density for a field border nesting species such as the grey partridge (Potts, 1980). The models were run in twenty five linear habitats, corresponding to lengths of 1, 2, 4, 8 and 16 kilometres each with widths of 2, 4, 6, 8 and 10 metres.

6.3 Results

6.3.1 Search patterns

The figures in this section graphically represent the search paths produced by each of the search algorithms. Examples of search paths generated by algorithms 1, 2 and 3 in a four hectare habitat are shown in Figures 6.8 to 6.12 presented in this section. The final two figures in this section show examples of search paths produced by algorithm 4 in a linear habitat six metres wide and one kilometre long. In all figures, nests are represented as red dots.

The search path generated by algorithm 2 shown in Figure 6.13 reveals a property of all the search algorithms: the sub-routine used to keep the search path within the nesting habitat sometimes concentrates search close to the habitat edge, especially near corners. Since observations of foxes foraging in lapwing nesting sites showed that they frequently moved along habitat edges, the bias generated by this artefact may actually contribute to the realism of the model.

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Figure 6.12 The first 200 straight line movements of a search path generated by algorithm 1. This algorithm generates relatively inefficient search paths that show a tendency to remain in previously searched areas. Red dots represent nests.

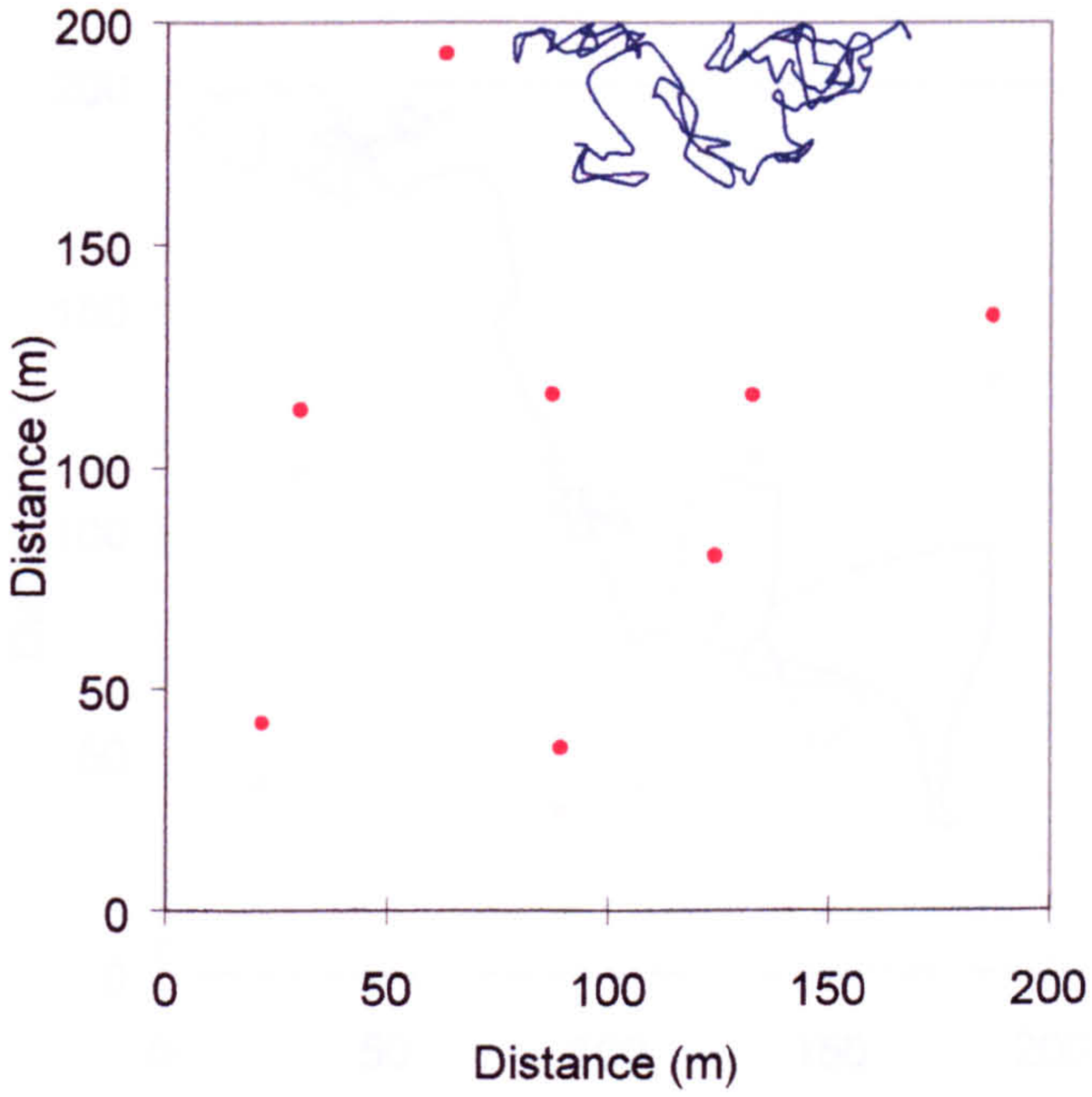


Figure 6.13 The first 200 moves of a search path generated by algorithm 2a. Following the detection of cues indicating the presence of nests, the search tactic changes to 10 movements of convoluted search. In the absence of cues, the searcher maintains a direct search path. Note that search is concentrated in the corner of the habitat due to the habitat-edge response. See text for explanation.

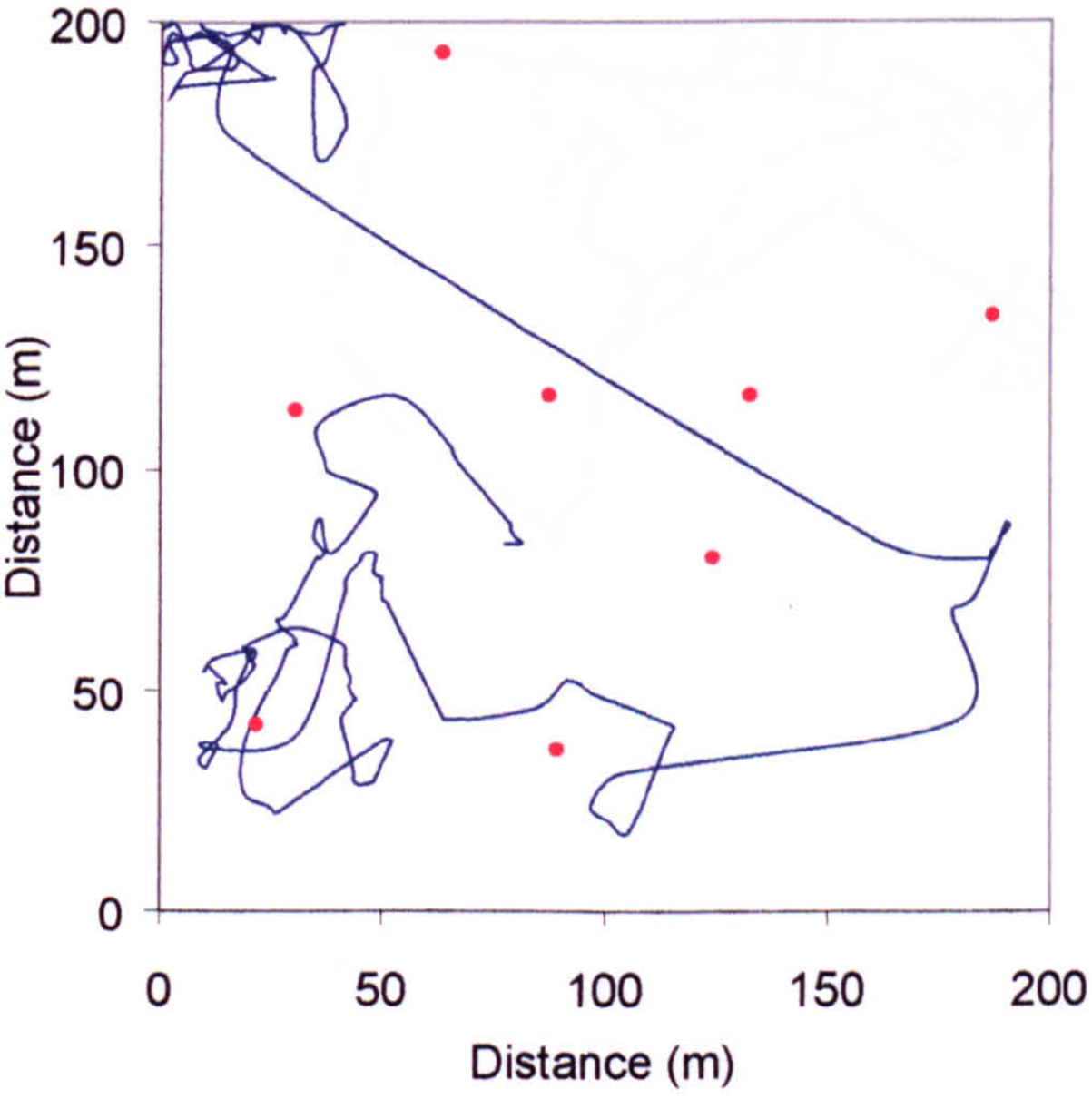


Figure 6.14 The first 200 moves of a search path generated by algorithm 2b. Following the detection of cues indicating the presence of nests, the search tactic changes to 40 movements of convoluted search. Note the two clusters of site restricted search close to nests.

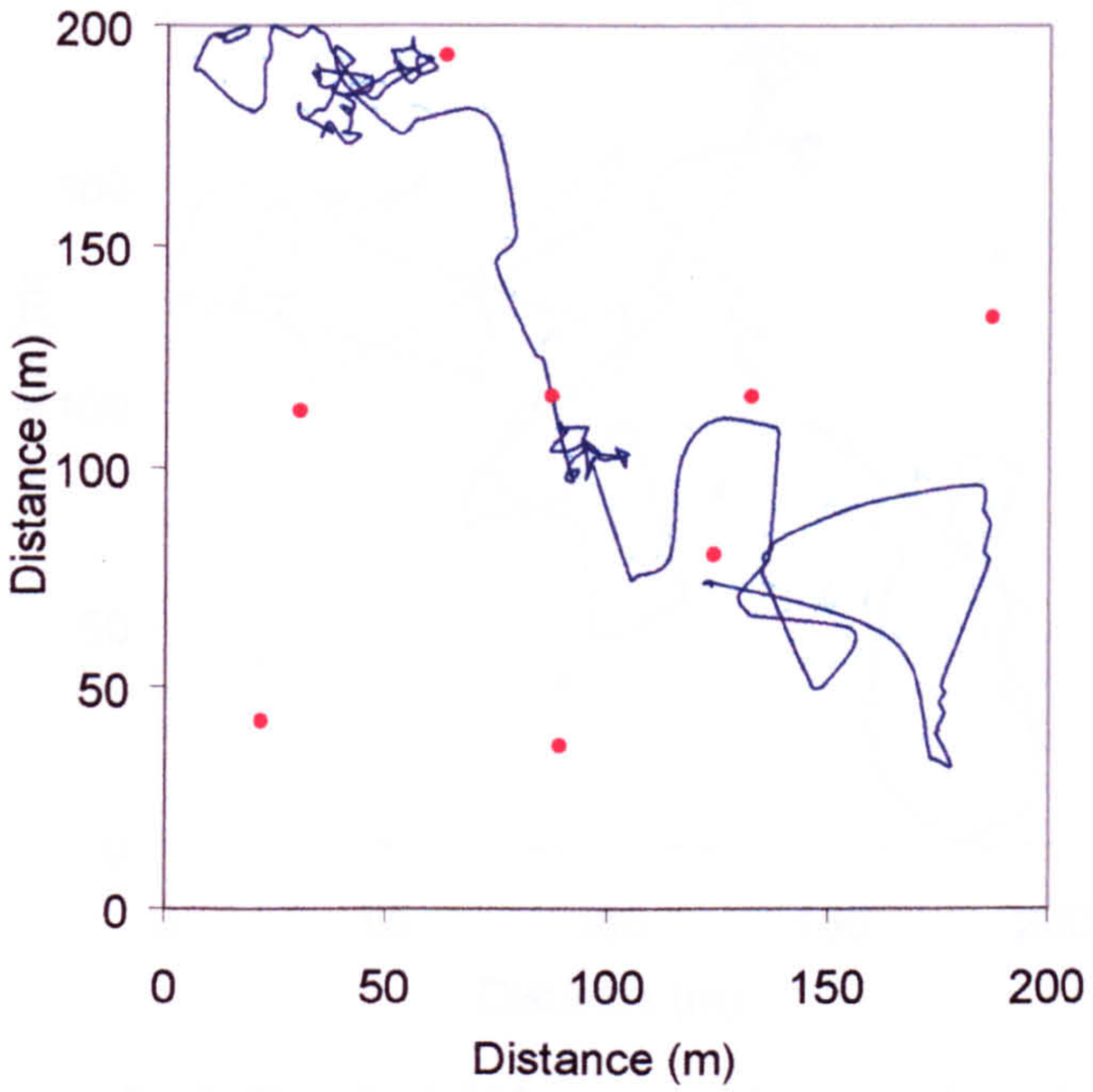


Figure 6.15 The first 200 moves of a search path generated by algorithm 3a. Following the detection of cues indicating the presence of randomly placed alternative prey, the search tactic changes to 10 movements of convoluted search. Note that site convoluted search paths are not associated with nests.

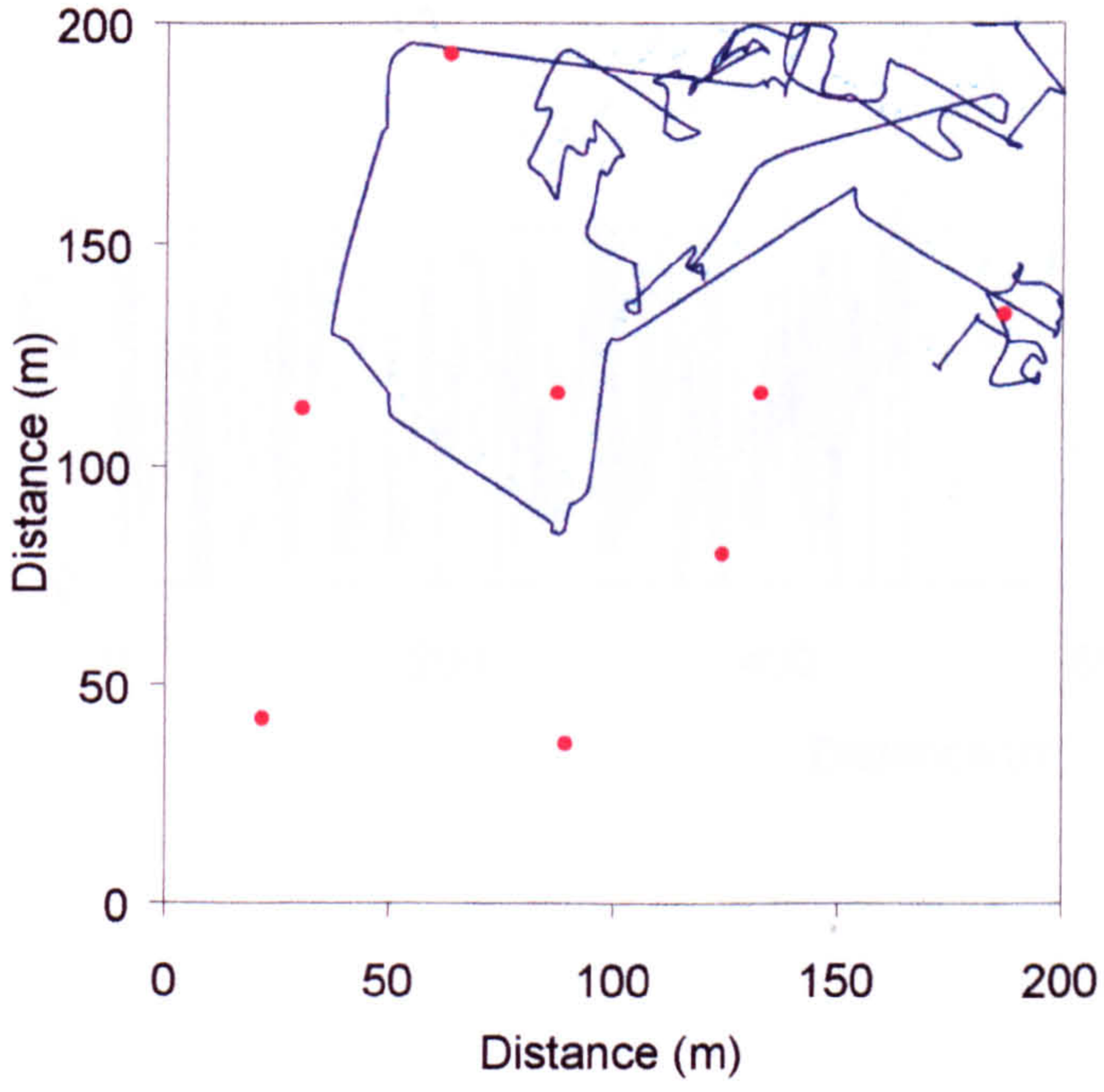


Figure 6.16 The first 200 moves of a search path generated by algorithm 3b. Following the detection of cues indicating the presence of randomly placed alternative prey, the search tactic changes to 40 movements of convoluted search.

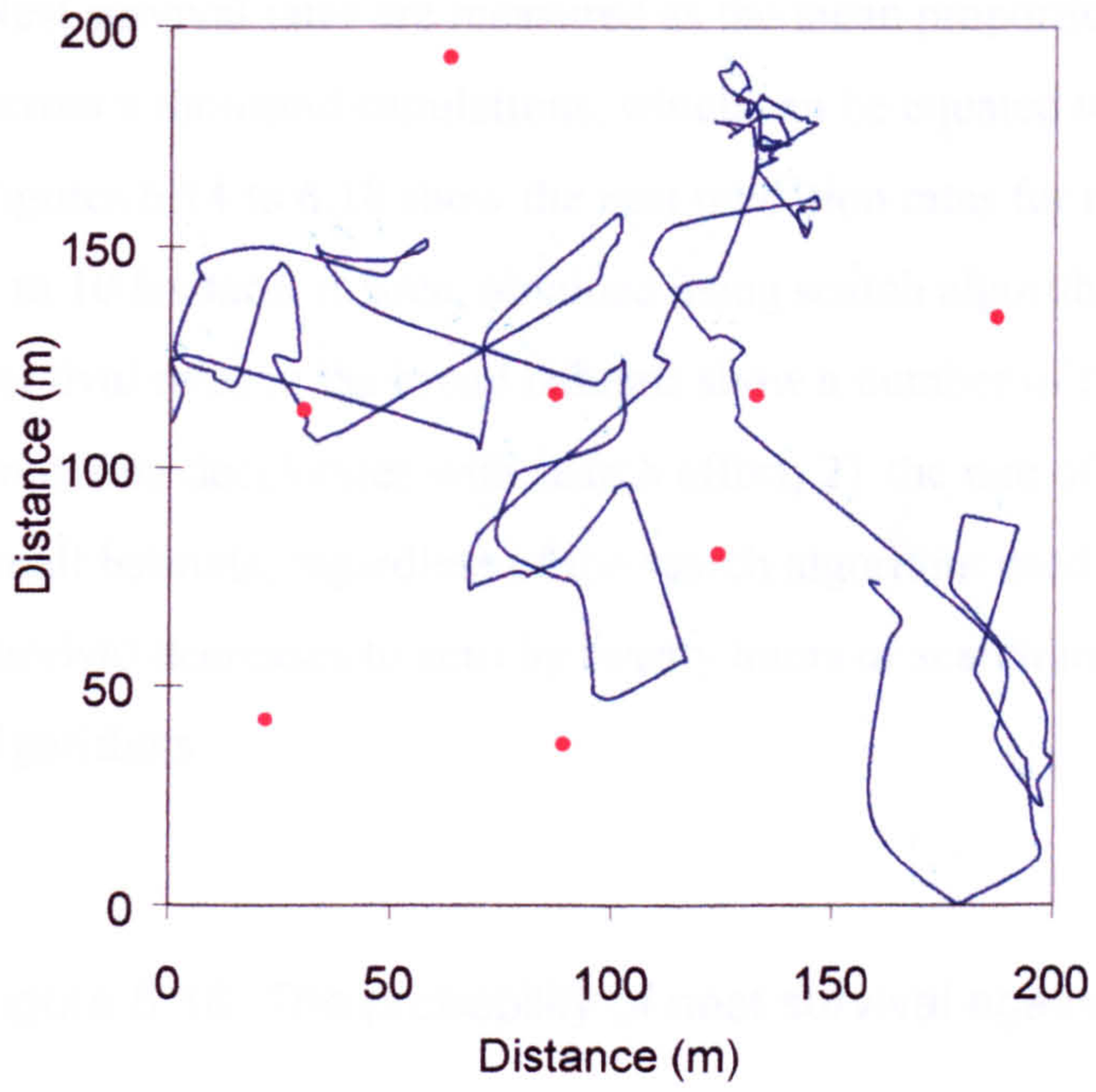
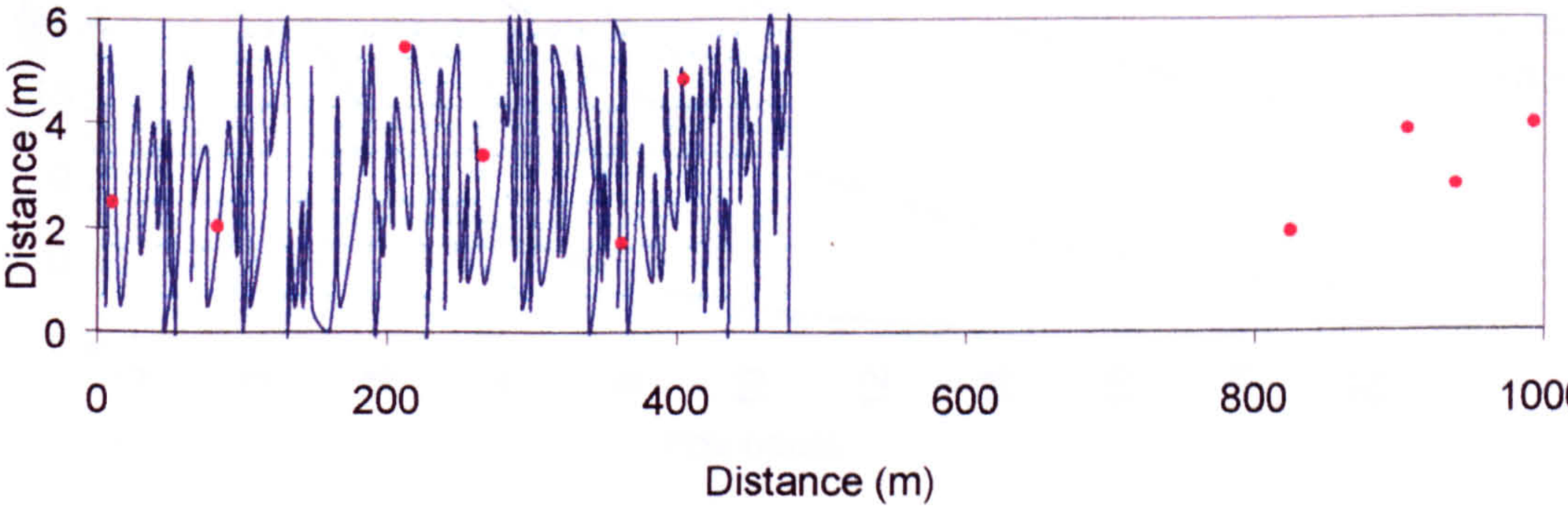


Figure 6.17 The first 200 moves of a search path along a linear habitat using algorithm 4. The zigzag path is generated by confining moves to consecutive 3 m wide strips of linear habitat. In algorithm 4b, the zigzag path is generated by confining moves to consecutive 6 m wide strips of linear habitat.



6.3.2 Nest predation rates

Nest survival rates are measured as the mean proportion of nests surviving per time period across a thousand simulations, which can be equated to the probability of nest survival. Figures 6.14 to 6.18 show the nest predation rates for nests in broad habitats varying from 1 to 10 hectares in area, obtained using search algorithms 1, 2 and 3. The pattern of nest survival rates in the broad habitats show a number of common features: 1) the rate of nest predation decelerates with search effort; 2) the rate of nest predation is always higher in small habitats, regardless of the search algorithm used; and 3) the probability of nest survival decreases to zero by twenty hours of search in 1 hectare habitats for all search algorithms.

Figure 6.18 The probability of nest survival against search effort using algorithm 1.

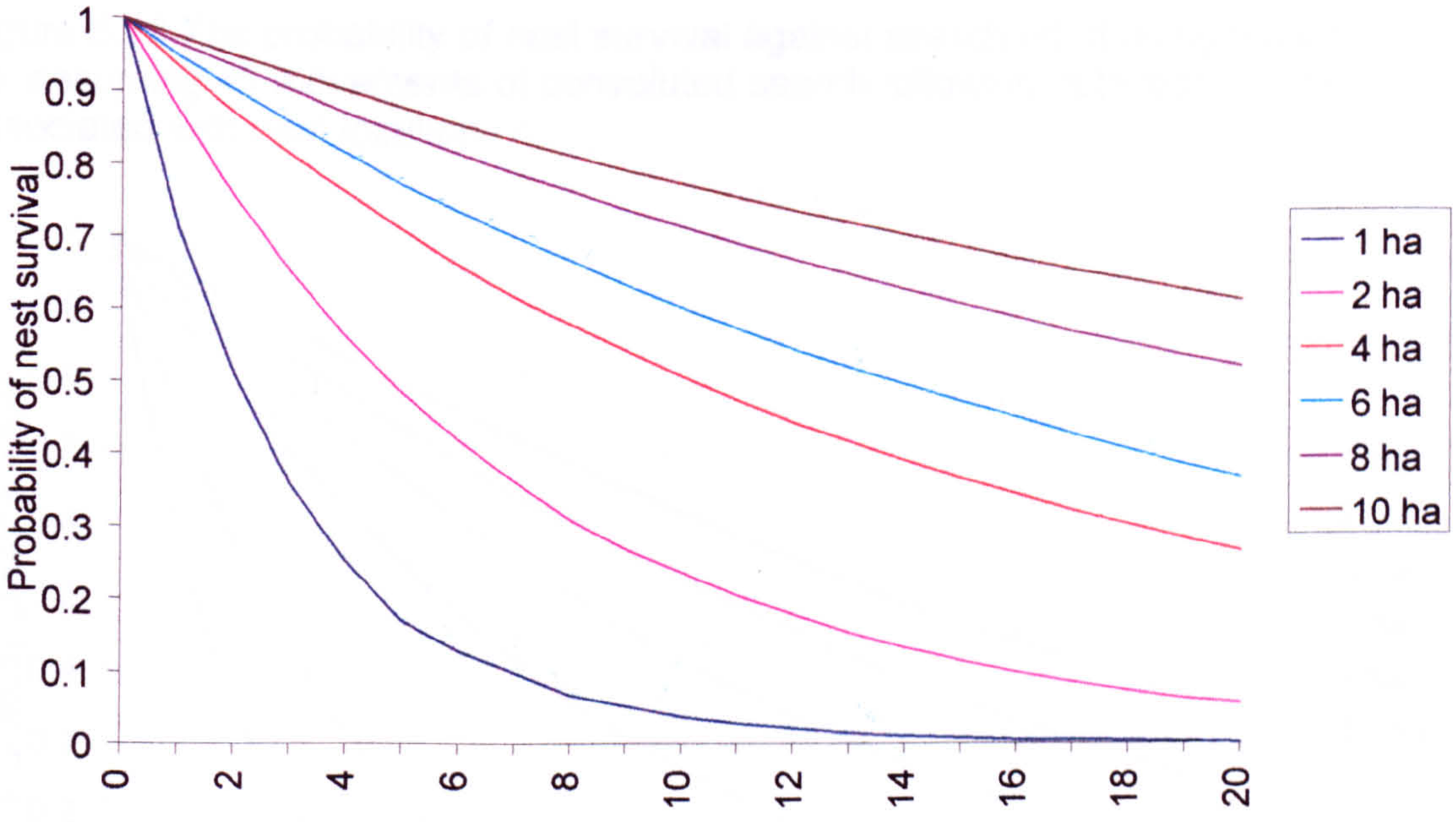


Figure 6.19 The probability of nest survival against search effort using algorithm 2a, assuming 10 movements of convoluted search following detection of cues associated with nest location.

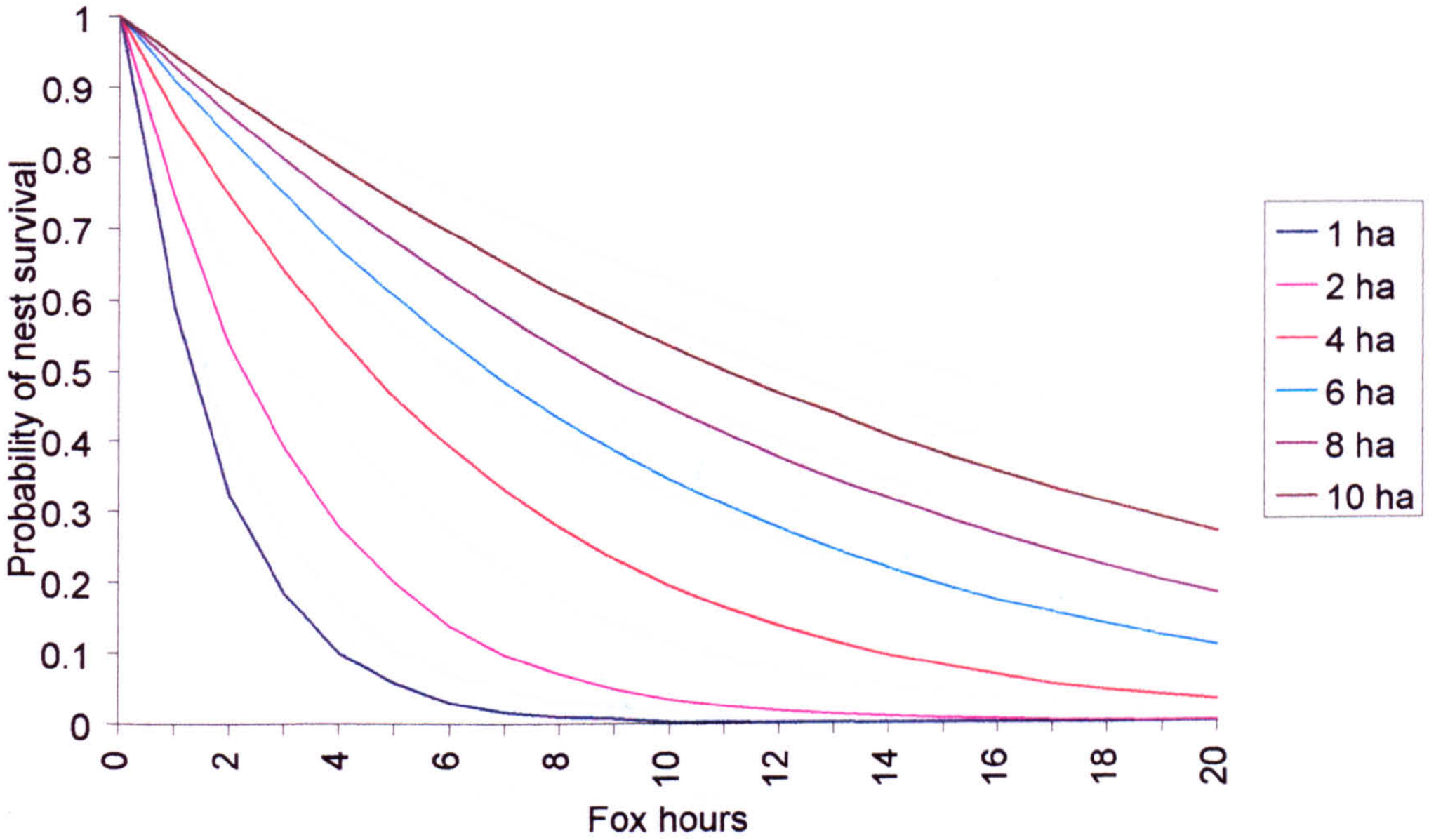


Figure 6.20 The probability of nest survival against search effort using algorithm 2b, assuming 40 movements of convoluted search following detection of cues associated with nest location.

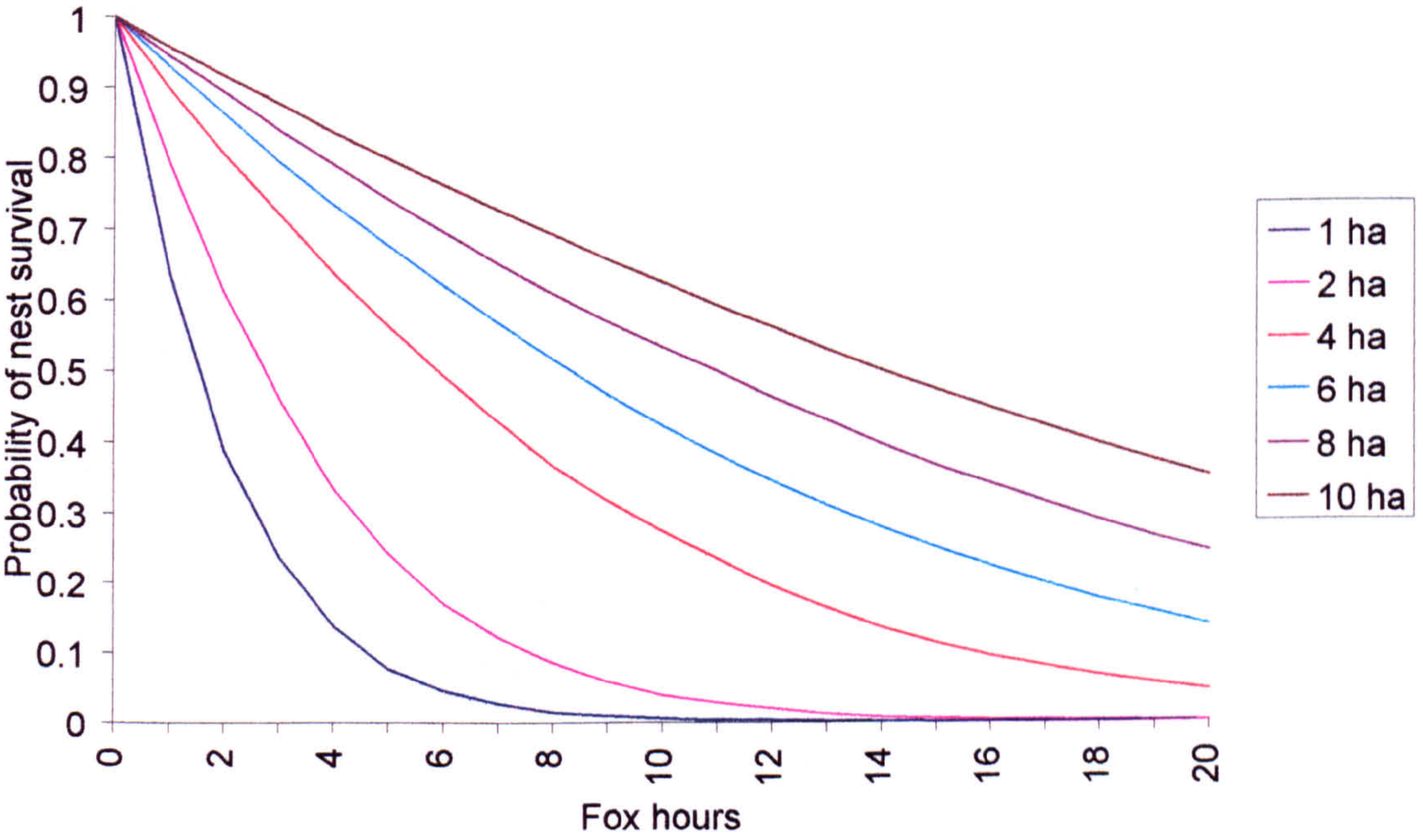


Figure 6.21 The probability of nest survival against search effort using algorithm 3a, assuming 10 movements of convoluted search following detection of cues associated with the location of independently distributed alternative prey.

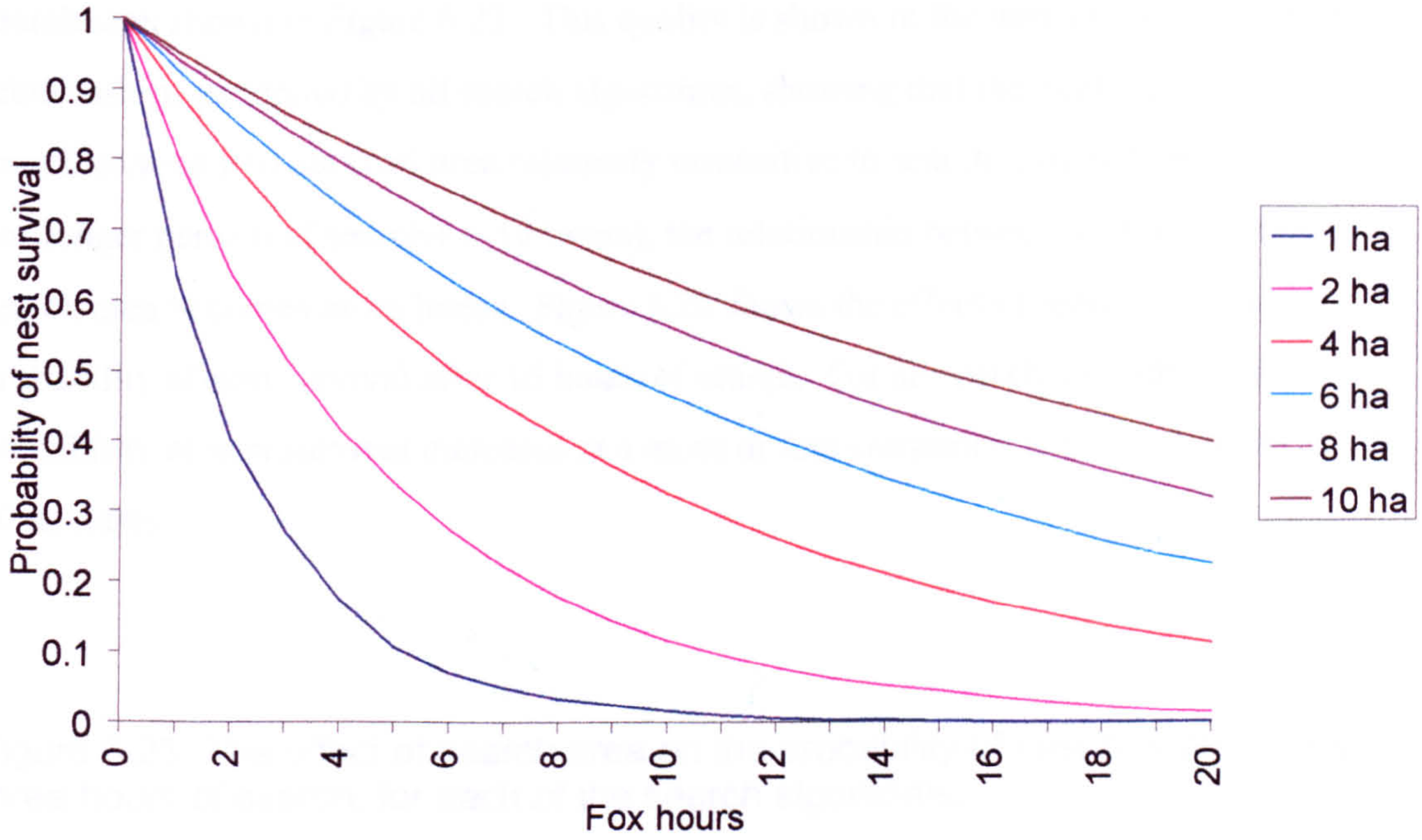
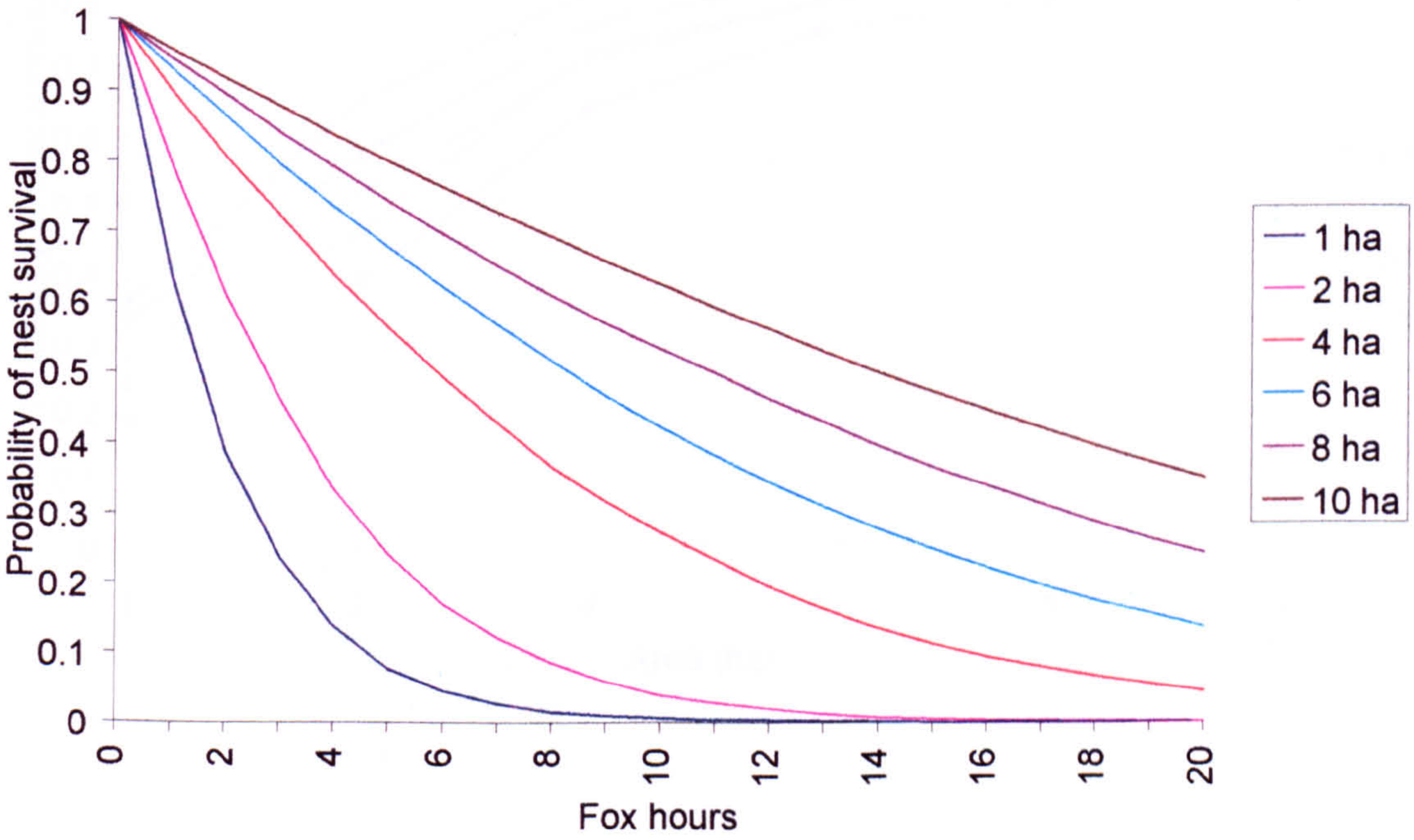


Figure 6.22 The probability of nest survival against search effort using algorithm 3b, assuming 40 movements of convoluted search following detection of cues associated with the location of independently distributed alternative prey.



The effect of search area on the rate of nest predation depends on search effort. For relatively short periods of search (1- 8 hours), nest predation is disproportionately high in 1 and 2 hectare search areas, as shown by the curved relationship between survival and search area shown in Figure 6.23. This quality is shown in the nest survival-search area relationships generated by all search algorithms, showing that the qualitative effects of search area on nest survival area relatively insensitive to search assumptions.

For longer periods of search (> 10 hours), the relationship between nest survival and search area becomes more linear. Figure 6.24 shows the effect of search area on the probability of nest survival after 16 hours of search. For all search algorithms, the probability of nest survival increases at a more or less constant rate between areas of 1 to 10 hectares.

Figure 6.23 The effect of search area on the probability of nest predation after three hours of search, for each of the search algorithms.

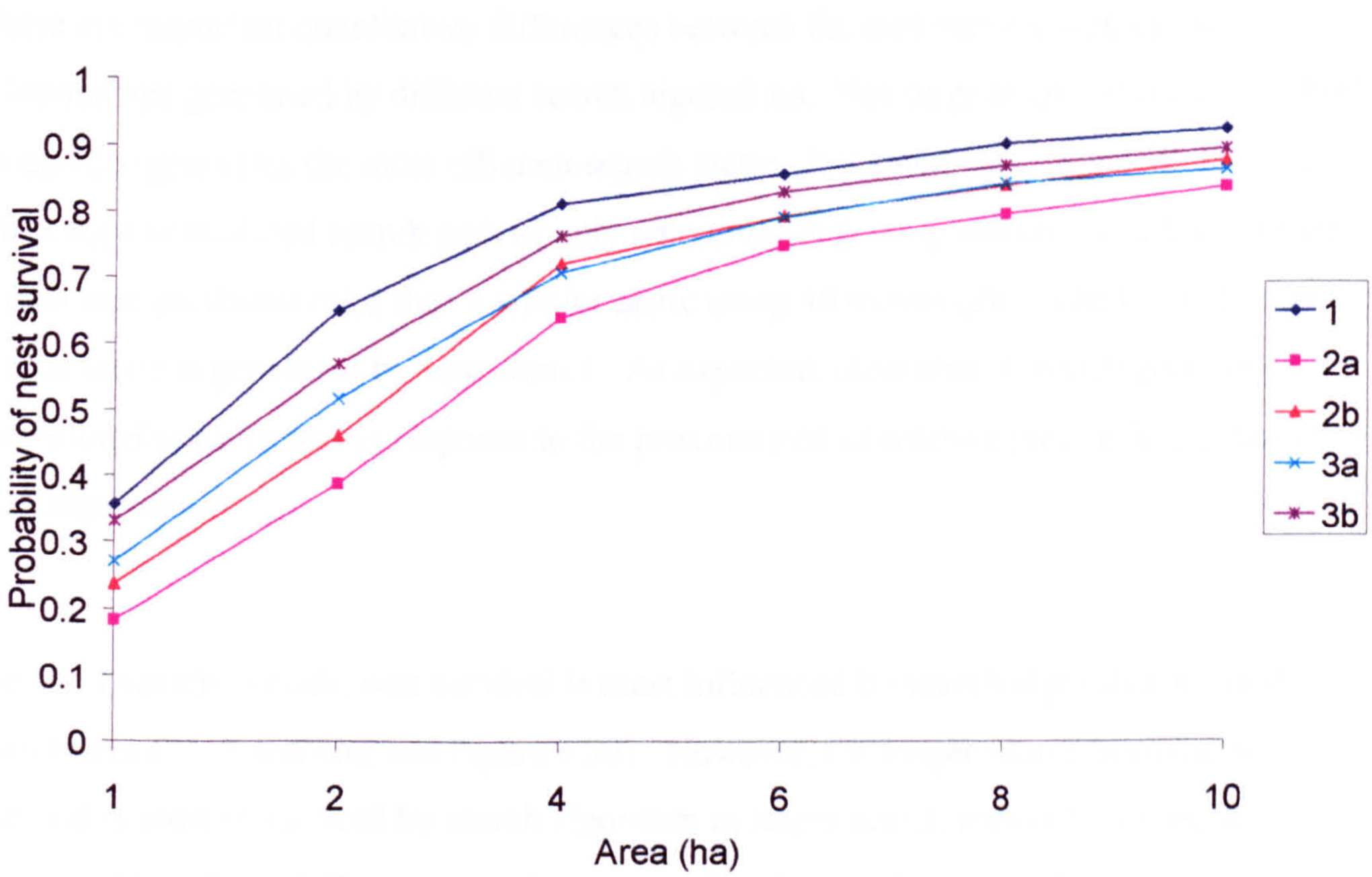
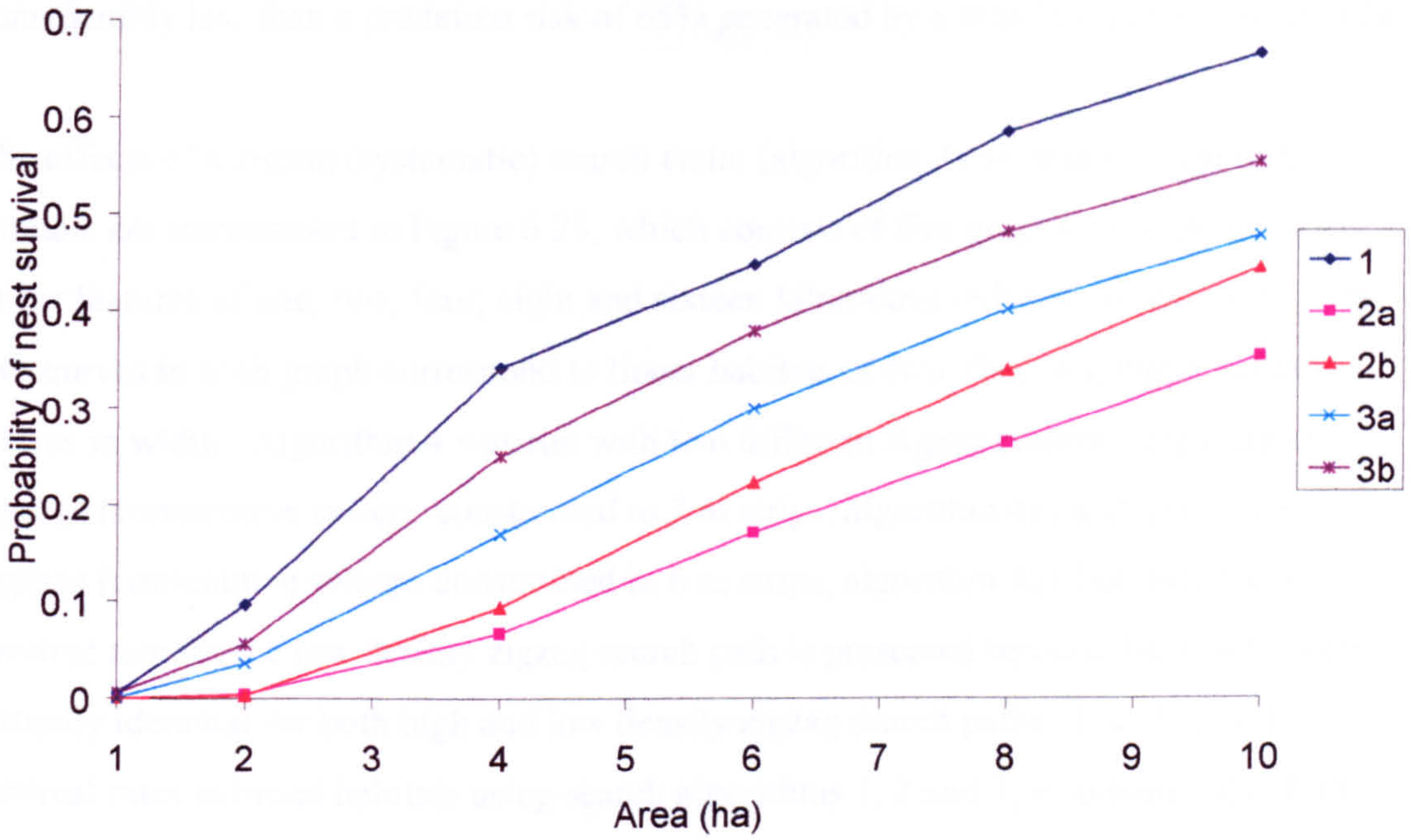


Figure 6.24 The effect of search area on the probability of nest predation after 16 hours of search, for each of the search algorithms.



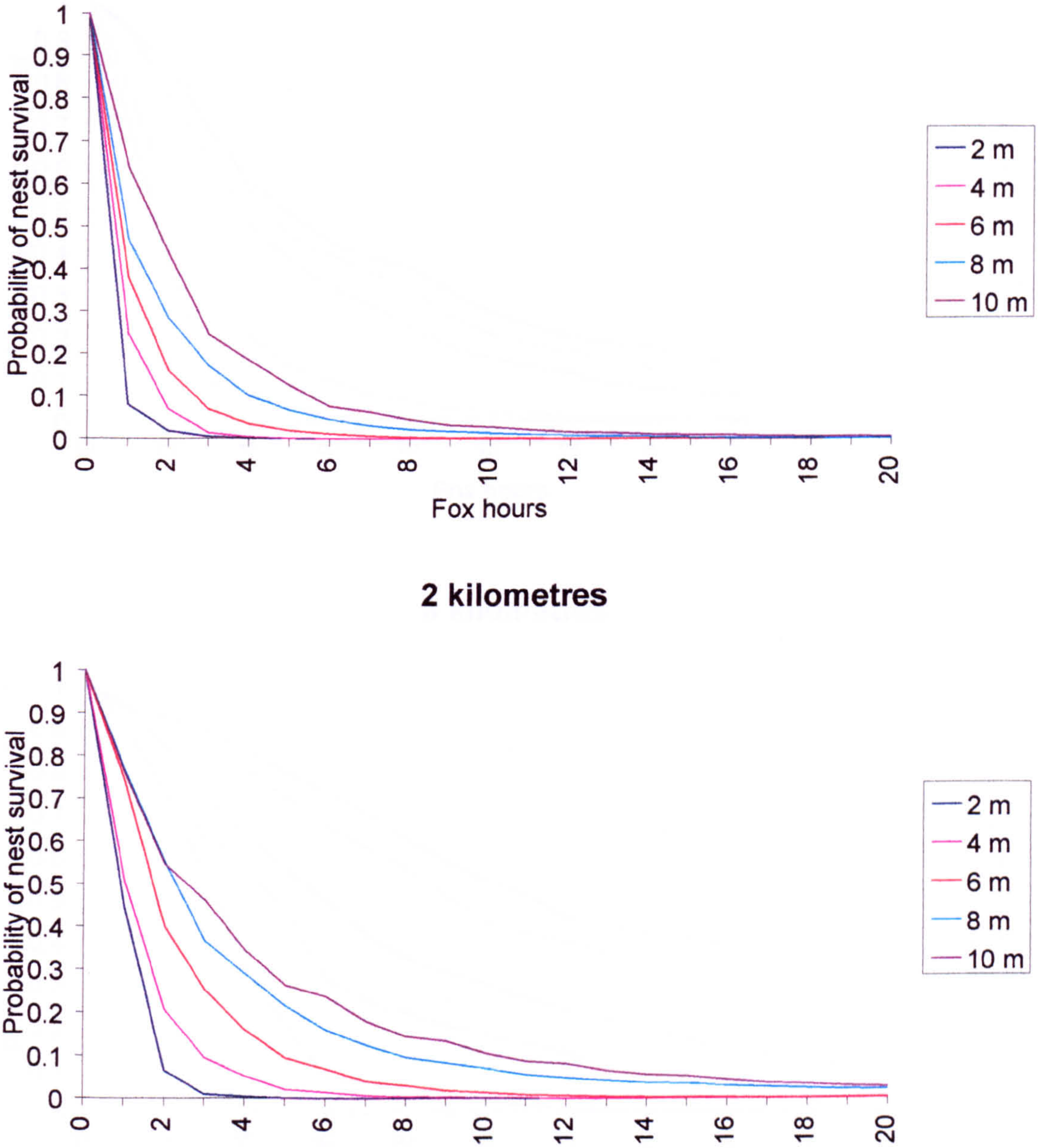
There are important quantitative differences between the nest survival-search area relationships generated by different search algorithms. Not surprisingly, algorithm 2 (both 2a and 2b) generates the most efficient search tactic. It is interesting to note that a tactic adopting a convoluted search path of only ten moves following search cues (2a) generates higher nest predation rates than a similar tactic using 40 moves (2b). The least efficient search tactic is generated by algorithm 1. As expected, algorithm 3, which generates convoluted search paths in response to the proximity of alternative prey, is less efficient than algorithm 2.

For short search periods, nest survival is most influenced by search algorithm in small search areas (1, 2 and 4ha; see Figure 6.23). However, for longer search periods, nest survival is most influenced by search algorithm in larger search areas (4 - 10 ha; see Figure 6.24). These differences are large enough to have a dramatic effect on nest survival. For example, after 3 hours foraging in a one hectare search area, the probability of nest predation by a searcher using algorithm 1 is 64% compared with a predation risk of

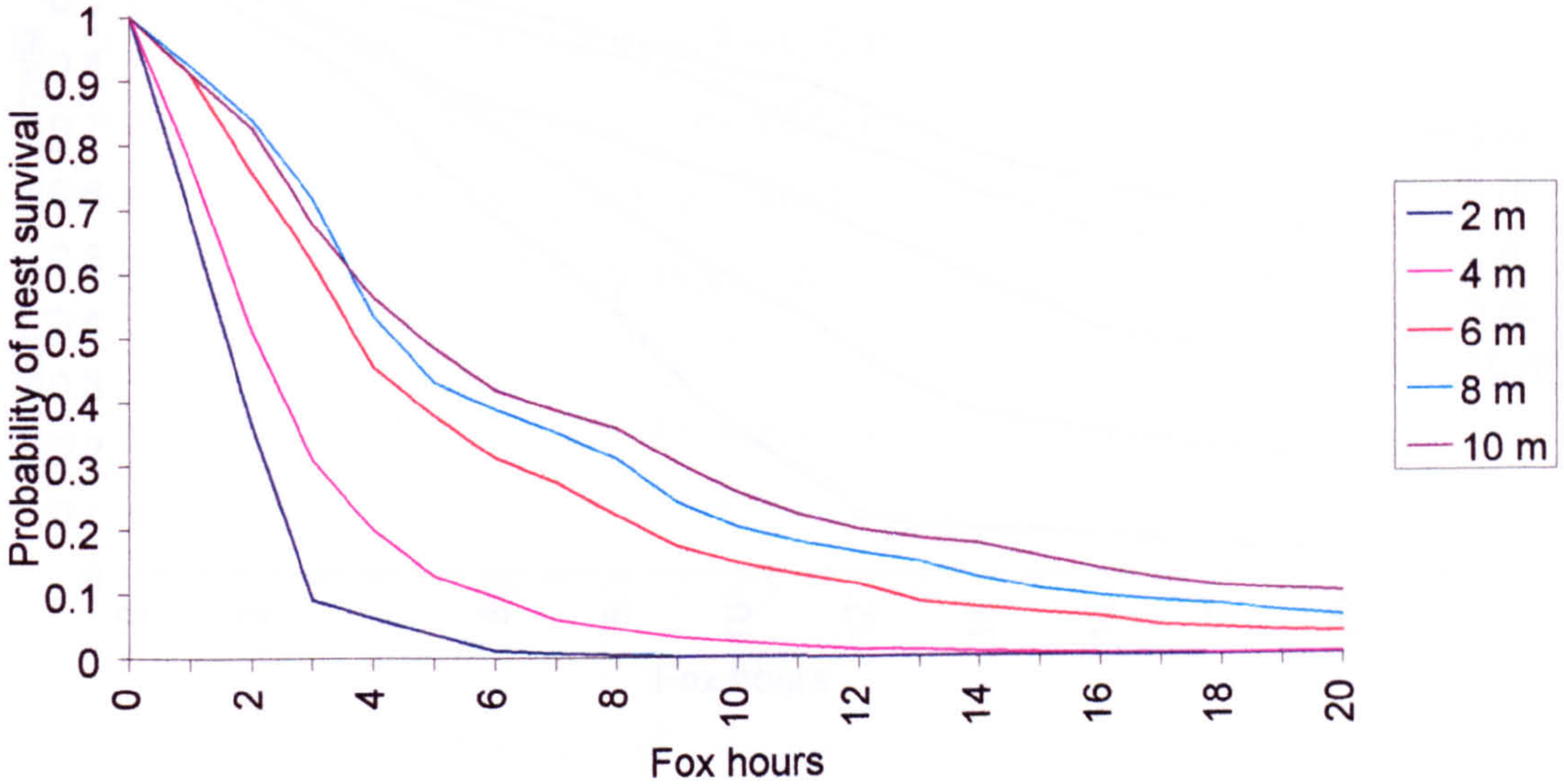
82% from a searcher using algorithm 2a. After 16 hours foraging in a 10 hectare nesting habitat, the risk of nest predation by a searcher using algorithm 1 is only 33%, which is considerably less than a predation risk of 65% generated by a searcher using algorithm 2a.

The effects of a zigzag (systematic) search tactic (algorithm 4) on nest survival in linear habitats are summarised in Figure 6.25, which consists of five graphs corresponding to linear features of one, two, four, eight and sixteen kilometres in length respectively. The five curves in each graph correspond to linear habitats of two, four, six, eight and ten metres in width. Algorithm 4 was run with two different zigzag patterns, high density zigzags (consecutive sweeps constrained to 3 m strips, algorithm 4b) and low density zigzags (consecutive sweeps constrained to 6 m strips, algorithm 4a), but only the nest survival rate for the low density zigzag search path is presented because the results were virtually identical for both high and low density zigzag search paths. Like the nest survival rates in broad habitats using search algorithms 1, 2 and 3, systematic search in linear habitats results in decelerating rates of nest predation with time. However, unlike nest predation in the broad habitats, the deceleration of nest predation rate is not smooth. Since each scenario uses the same nest distribution per simulation and the simulated fox always searches the linear habitat in the same direction, the probability of nest encounters will be clustered in time, resulting in kinked nest survival curves. Not surprisingly, nest predation rate was higher in narrower and shorter habitats. In short habitats ($\leq$ 4 km), long search times (> 15 hours) would lead to low nest survival (< 15%) regardless of habitat width. In longer habitats ($\geq$ 8 km), the width of the habitat had a big effect on nest survival. For example, a systematically searching predator that spent a total of 20 hours foraging along a 16 km $\times$ 2 m habitat throughout the nesting season, would be expected to predate 97% of all nests in the habitat. However, the same predator exerting the same foraging effort (i.e. 20 hours search during the nesting season) in a 16 km $\times$ 10 m habitat, would be expected to predate only 47% of the nests.

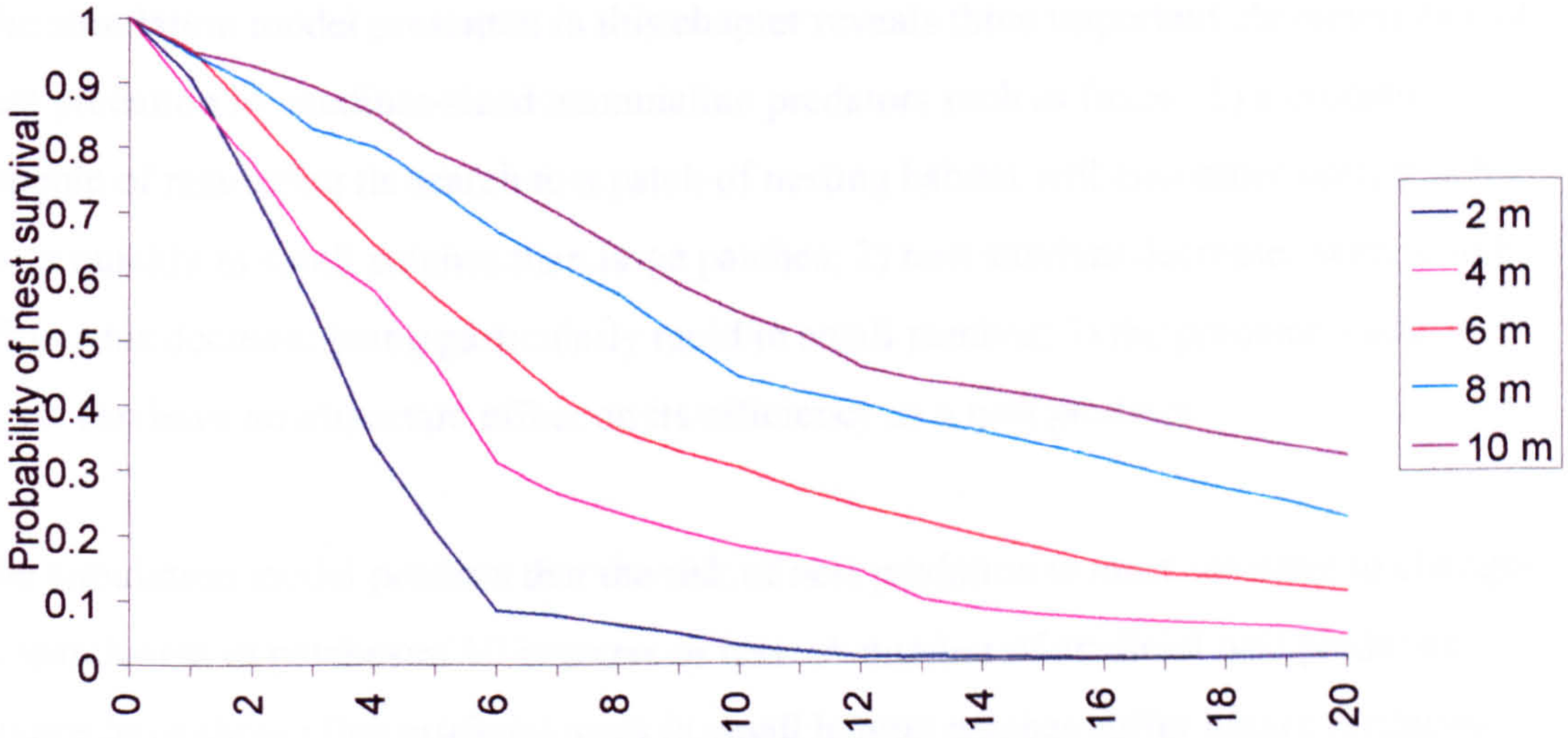
Figure 6.25 The effect of the length and width of linear search areas on the probability of nest predation.



4 kilometres



8 kilometres



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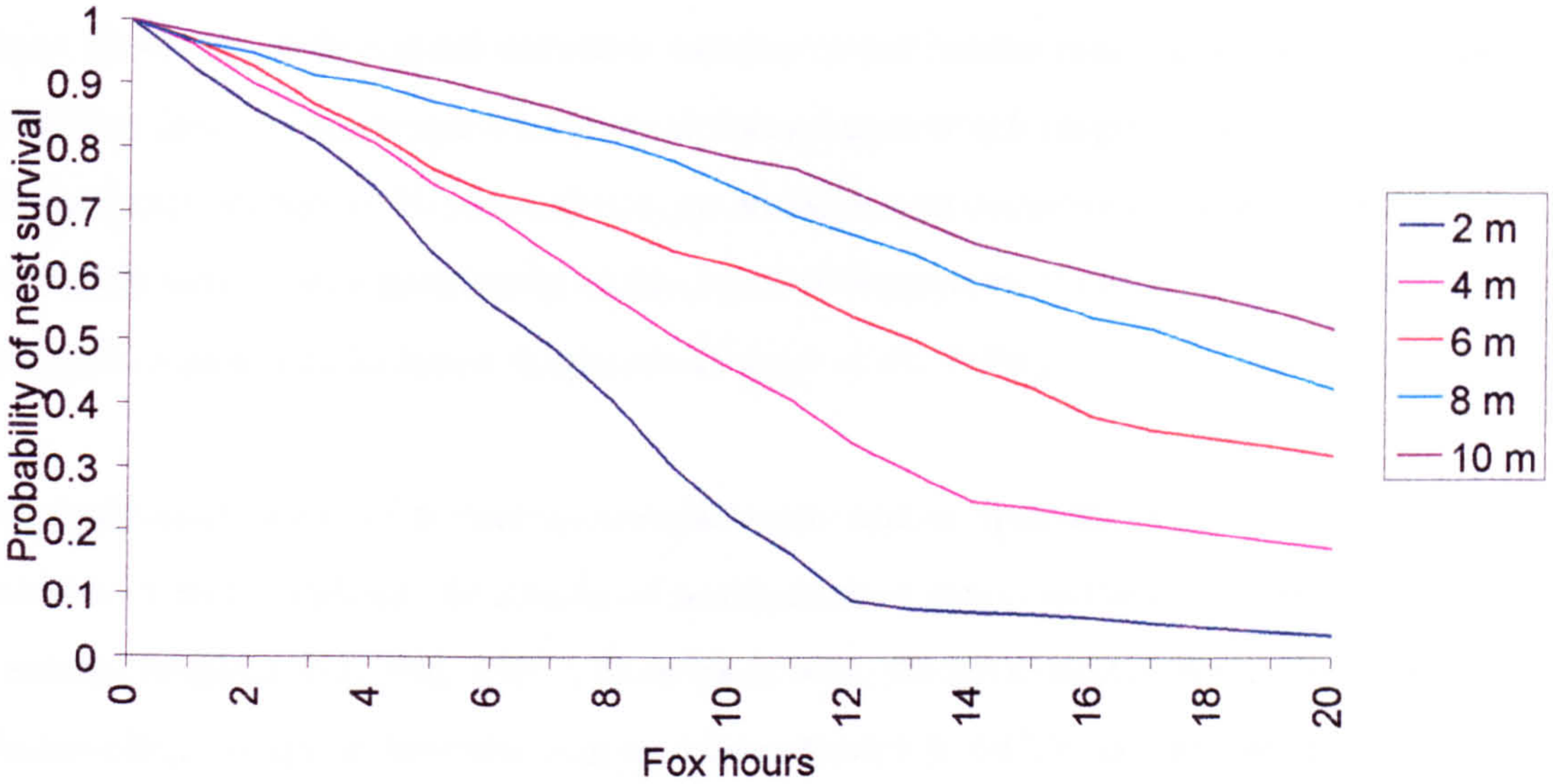

6.4 Discussion

The simulation model presented in this chapter reveals three important characteristics of nest predation by medium-sized mammalian predators such as foxes: 1) a predator capable of restricting its search to a patch of nesting habitat will encounter nests much more quickly in small patches than large patches; 2) nest survival decreases with search effort, this decrease being particularly rapid in small patches; 3) the predator's search tactic can have an important effect on its efficiency as a nest predator.

The simulation model predicts that the risk of nest predation is most sensitive to changes in search area in patches of 10 hectares or less. A number of artificial nest predation studies have shown that artificial nests in small habitat patches suffer higher predation rates than those in larger habitat patches (Paton, 1994; Major & Kendal, 1996). For example, Wilcove (1985) found that artificial nest predation was significantly lower in very large tracts of forest (all greater than 280 ha) than small tracts. Generalist mammalian predators including red foxes were present at all the sites, and raccoons,

mammalian predators including red foxes were present at all the sites, and raccoons, opossums *Didelphis virginiana* and striped skunks were all known to have robbed eggs from artificial nests, so mammalian predators were a potentially important source of nest loss. However, Wilcove did not show whether or not habitat area was an important factor affecting nest predation rate within small forest tracts which ranged from 3.8 - 13.3ha. In the tallgrass prairies of North America, an artificial nest experiment showed that egg predation rates were significantly higher in small fragments of prairie less than 15 hectares in area than in larger fragments (Burger *et al.*, 1994).

Semipalmated plovers *Charadrius semipalmatus* nest on sparsely vegetated shingle habitats in arctic regions. In a study of semipalmated plover nesting success in northern Canada (Armstrong & Nol, 1993), these birds were shown to nest either on the coast of Hudson Bay on gravel beaches ranging in area from 1 to 647.9 hectares (median 12.9 ha), or further inland on smaller patches of gravel, ranging from 0.007 to 28.7 hectares (median 0.79). Nest predation was significantly higher in inland areas where nesting patches were much smaller (40% predation, $n = 35$) compared with the rate of nest predation in coastal areas (11.5% predation, $n = 26$) were relatively large. However, it is not possible to determine from these data whether or not this effect is brought about by site or the size of nesting patches. Both red foxes and arctic foxes were shown to be active in the study sites. In Norwegian uplands, Byrkjedal (1980) showed that artificial nests in small snow-free patches of suitable wader nesting habitat suffered significantly higher predation rates than nests in larger snow-free patches. Red foxes were thought to have been responsible for the majority of nest loss early in the nesting season when the patches of snow-free area suitable for nesting were rarely larger than two or three hectares. Later in the nesting season only patches of snow remained, leaving large areas of snow-free ground available for nesting waders. During this period the majority of artificial nests were robbed by ravens *Corvus corax*. Because of the scale and prominence of nesting patches in this study, it provides some of the best evidence supporting the predictions of the model.

A study of the nesting success of gadwalls in wetlands in Utah showed that patch size (the area of plant species association type where each nest was located) was negatively related to nest predation (Crabtree *et al.*, 1989). These nesting patches were of a considerably smaller scale than those patches considered in the other studies mentioned here, measured in square metres rather than hectares. Striped skunks were the main egg predators in this study, but weasels and red foxes also robbed some nests. Nocturnal observations showed that skunks spent 30% of their time foraging in the narrow band of vegetation close to the water's edge where many of the gadwalls nested indicating a habitat restricted search.

Nests in small patches can suffer heavy losses to mammalian predators. On a 5.2 hectare island situated in Lake Audubon in North Dakota, 22 out of 23 Wilson's phalarope nests were predated along with numerous waterfowl nests (Kagarise, 1979). Although it was not known which predators were responsible for nest loss, several mammalian predators including raccoons and American badgers were known to have visited the island. Some waders, such as avocets, nest on small islands in shallow lagoons. At Northward Hill R.S.P.B. reserve in north Kent in 1996, 17 avocet *Recurvirostra avosetta* nests were laid on 12 islands in a shallow pond, ranging in area from 0.0003 ha to 0.0312 ha (mean, 0.0137 ha). A fox, identified from footprints, caused 100% breeding failure in the avocet colony in a single night (K. Parker, pers. comm.).

The width of linear habitats has been shown to affect the predation rate of real nests. For example, Crabtree *et al.* (1989) showed that dikes on which gadwalls nested were significantly wider around successful nests than predated nests. In Finland, the rate of predation on Temminck's stint nests was approximately 70% on thin beaches, but less than 50% on wide beaches that were at least 100 metres in width (Koivula & Rönkä, 1998). Lessells (1984) studying the mating system of snowy plovers at a study site in the south of France discovered that nest success at this site was around 10% ($n = ca.700$), with the majority of losses due to predation. These plovers nested on a system of dykes

separating saltpans, and Lessells hypothesised that predation rates on the dykes 'may be high because predators find these areas easy to sarch systematically'.

Not all field studies support the qualitative predictions of the model. A study carried out in the forests of the eastern United States showed that the area of forest patch (ranging from 9 - 203 ha) and the area of clearcuts (ranging from 2 to 107 ha) had no effect on the predation rate of artificial ground nests, despite the presence of generalist mammalian predators including red foxes, racoons and striped skunks (Rudnicky & Hunter, 1993). In forests in the Bavarian Alps where stands of various age classes form a mosaic of patches ranging from 1 to 30 hectares, the predation rate of artificial ground nests was not influenced by the area of the patch, despite the fact that the majority of predated eggs were taken by mammalian predators including red foxes (Storch, 1991).

There are a number of reasons why these studies did not detect any effect of patch size on nest predation. For example, it is possible that predators perceive some habitat patches in a different way than researchers, leading to incorrect measurements of patch area. Although foxes and skunks, both well known egg predators, have been observed to restrict their search to the nesting habitats of some ground nesting species (Crabtree *et al.*, 1989), they may not always recognise the boundaries of the nesting habitat of all ground nesting species.

The model predicts that the rate of nest predation is sensitive to foraging effort, especially in smaller habitats. Predation risk increases rapidly in the first few hours of search effort, and relatively small changes in foraging effort can have a large effect on nest predation rate. A number of factors can influence the time spent foraging in a patch. Foraging theory predicts that a forager should leave a patch when its instantaneous rate of energy gain drops below the average net rate of energy that can be gained from its territory. In other words, variation in the distribution and abundance of other prey types across patches would be expected to influence the search effort in any given patch. This may cloud the effect of search area on nest predation rate, so it is not surprising that the effects

of search area are difficult to determine in the field. High densities of other prey types in nesting habitats have been shown to lead to high nest predation rates. For example, Vickery *et al.* (1992) found that there was a correlation between invertebrate-foraging activity by striped skunks and predation of grassland passerine nests, suggesting that the availability of invertebrates in the nesting sites increased incidental nest predation.

The model shows that search tactics can have an important effect on nest encounter rate. Search tactics may be expected to differ between species or even individuals within a species. The search tactic of generalist predators such as red foxes, skunks and racoons may vary depending on which habitat and prey types they have experienced. The optimum search tactic will depend on the relative density of prey. For example, a fox in a territory with a high density of rabbits in one place may forage most effectively by employing a sit-and-wait ambush tactics to catch fast moving rabbits, whereas a fox in a territory with small and dispersed food items such as insects, nests and scavenge will be better off using a widely ranging and systematic search tactic.

The results of the model have a number of implications for the management of nesting habitats to reduce predation. The changes in nest predation form 1 to 4 hectares are very large regardless of the assumed search tactics. Nest predation by mammals in small nesting habitats of a hectare or less in area may be reduced by increasing the nesting habitat area by a few hectares. The addition of two or three hectares of nesting habitat would be a perfectly feasible management strategy in such cases, both in terms of effort and cost. Perhaps the main problem lies in correctly identifying the nesting habitat patch perceived by predators. In some cases, where the border of a nesting habitat is obvious, such as the dense herbaceous vegetation in which many dabbling ducks commonly nest, patches of nesting habitat will be easy to identify. In other cases, the borders of nesting habitat are not so obvious to human observers. Waders like curlews, redshank and lapwings may have preferences for particular patches of habitat or locations within a tract of grassland that are not immediately clear to human observers. Theoretically, an increase in width of a few metres to linear habitats such as vegetated river margins or

dikes, may considerably reduce the rate of nest predation by systematically searching predators. The lengths of linear habitats also has a potentially important impact on the risk of nest predation by systematically searching predators, though in most cases it is probably more practical to alter the width of linear nesting habitats than the length. The model shows that nest predation rate is particularly sensitive to small changes in total search time between zero and around four hours of search, especially in smaller patches. Any management strategy that can reduce the time mammalian predators spend searching within nesting habitats may also be effective in reducing nest predation, especially if reductions in search time occur within the first critical few hours of search. Potentially, this could also be achieved by habitat management by creating habitats away from the nesting sites that promote higher alternative prey abundances within the local area, and therefore encourage the territorial predator to forage away from nest sites. This form of habitat management may be considered less practical by reserve managers with limited budgets or reserve area, and may also increase the density of some egg predators.

Before any of these management strategies are evaluated in the field, field experiments should be carried out to test the predictions of the model. In order to do this, artificial nest experiments may be set up, with nests deployed in a range of replicated patch sizes. In addition, the experimenter will need to be able to, 1) independently estimate relative search effort in different patches, using counts of tracks in soft ground (Johnson *et al.*, 1989) or on sooted panels (Oehler & Litvaitis, 1996), or indeed additional remote cameras not associated with nests; 2) use a suitable range of nesting habitat patch sizes, particularly patches from ranging from a few square metres in area to 10 hectares; and 3) show that predators are capable of restricting their search to the type of nesting habitat patches in the study using nocturnal observation. When determining the effect of patch area on the nest predation rate by mammalian predators, the predation rates in each patch should be corrected for relative search effort. This experiment would be able to determine whether or not patch size influences nest predation rate by mammalian predators, and also be able to determine the relative contribution of avian and other non-mammalian predators to nest predation. Artificial nests will be very different from real

nests in many ways, so the purpose of these experiments is not to extrapolate artificial nest predation rates to real nests, but rather to determine patterns of predation in relation to measured variables.

7. General discussion

Habitat structure can be an important factor influencing animal population dynamics (e.g. Gilpin, 1987) and may do so by altering species interactions in several ways (Fagan *et al.*, 1999). In particular, the interaction between predators and their prey can be strongly influenced by the spatial structure of habitats and the populations they contain. Predator-prey interactions may be stabilised by increasing habitat patchiness by providing spatio-temporal refugia for prey (e.g. Taylor, 1990), but can also de-stabilise predator-prey systems depending on the demography and behaviour of the predators and prey. For example, Kareiva (1987) found that increasing habitat patchiness lead to local insect prey population explosions, an effect brought about by the insect predator's reduced searching and aggregation efficiency in the patchy environment. In some vertebrate predator-prey systems, there is evidence to suggest that changes in habitat structure, particularly fragmentation, can lead to increases in prey consumption rate by predators. In particular, high rates of nest predation have been associated with features related to habitat fragmentation, such as increased proximity to habitat edges and decreased size of habitat patches (e.g. Wilcove, 1985; Paton, 1994; Hartley & Hunter, 1998). Habitat fragmentation can increase nest predation in three main ways: 1) by increasing predator abundance; 2) by increasing predator efficiency; and 3) by increasing the profitability of patches of nesting habitats as a foraging site, relative to other patches.

There is some evidence to suggest that egg predators are more abundant in fragmented habitats, such as mixed woodland-agricultural landscapes. Andrén (1992) showed that the total density of corvids and the predation rate on artificial nests was higher in agricultural habitats with forest fragments than in forest dominated landscapes. The densities of mammalian predators have also been shown to be higher in fragmented habitats: in New Hampshire, Oehler & Litvaitis (1996) showed that racoons and wild canids, including red foxes, were more abundant in diverse landscapes including agricultural and grass-brushland habitats. This effect has also been observed in Ontario,

where racoons were shown to be more abundant in areas with extensive agricultural edge and in woodland remnants in areas with extensive corn cover (Pedlar *et al.*, 1997). However, a similar study carried out in Illinois, found no difference between the activity and abundance of mammalian egg predators at forest-farm edges and forest interiors (Heske, 1995). Although more studies need to be carried out in different locations to draw general conclusions, generalist mammalian and avian predators appear to be successful in exploiting modern agricultural landscapes, which may be a result of increased resource availability or a reduction in natural enemies (mess-predator release). In Britain, there have been relatively few estimates of fox density in rural areas, and none that have related fox density to habitat fragmentation. In mixed farming habitat in southern England, Reynolds & Tapper (1995) found that the number of adult foxes per territory ranged from one to three. If these figures are typical for mixed lowland farming habitat in Britain, then the low density range implies that the maximum number of adult foxes foraging in any particular nesting habitat will be relatively constant in different locations. However, local fox removal, which is practised throughout Britain, may alter these densities (Reynolds *et al.*, 1993), and may hold fox densities below the carrying capacity imposed by the habitat. Thus, intense control efforts in Britain may mask any subtle effects of habitat structure on fox population density.

Alterations in the area and quality of patches of nesting habitat can affect the efficiency of the antipredator behaviour of nesting birds and the foraging efficiency of egg predators. Many ground-nesting birds space their nests out as a defence against mammalian predators in order to reduce the efficiency of site-restricted search following nest encounter (Page *et al.*, 1983; Hogstad, 1995). The results of the simulation model presented in this thesis show that the risk of predation of widely separated nests by a fox-like predator can be strongly influenced by small scale differences in habitat structure. Nests located in patches that range in size from zero to four hectares may be expected to suffer very different predation rates by foxes. Other small scale differences in habitat can influence the predator-nest interaction in other ways: the results in chapter 3 showed that lapwing nest predation was strongly influenced by the local crowding of nests, which in

turn must be affected by the spatial distribution of suitable nesting microsites. Thus, nesting habitats that decrease the density or size of breeding lapwing aggregations will reduce the effectiveness of communal anti-corvid nest defence. In addition, nest success can be influenced by differences in the quality of habitat. For example, Galbraith (1988) and Baines (1990), found that the predation rate of lapwing nests depended on the precise nature of the grasslands in which they nested. The increased nest predation on improved pastures noted by Baines (1990), may have been brought about by the increased visibility of nests against the more uniform background presented by improved pasture. This suggests that diurnal predators, particularly avian predators are more effective at finding nests in these habitats.

Changes in the height of vegetation around nest microsites may influence the ability of incubating waders to detect approaching predators. The early detection of predators and the early departure from nests may be an important strategy against predators such as foxes that may use flushing adults as a cue for changing search behaviour. Koivula & Rönkä (1998) have suggested that changes in habitat have reduced the efficiency of the anti-predator strategy of Temminck's stints in this way.

Nest predation in some bird species such as lapwings can be highly variable between sites with similar habitats and predator communities (Table 2.3, Table 3.1). The results presented here suggest that small scale differences in habitat quality and fragmentation can have an important influence on nest predation, and this may help to explain why there is so much variation in nest success between sites of similar habitat types and predator communities. Different predator species are likely to vary in their nest foraging efficiency with respect to local habitat structure. The simulation model presented in chapter 6 showed that the rate of nest predation was strongly influenced by the search tactic used, showing that even relatively small differences in search behaviour can have a large impact on nest predation.

An important factor linked to habitat structure and predator foraging behaviour, is the overall distribution and abundance of prey. Foraging theory predicts that an increase in the abundance of alternative prey will lead to a decrease in the rate of nest predation, a prediction that has been supported by field observations (Schmidt, 1999). In addition, the relative costs and benefits of searching and consuming eggs will differ in contrasting predator types such as corvids and medium-sized mammalian predators, so these predators are expected to respond differently to the abundance of alternative prey types. The relative distribution and abundance of the prey of foxes is likely to vary from site to site. In Britain, the abundance of important prey species such as rabbits and small mammals will vary spatially due to differences in farming practise (Rogers & Gorman, 1995; Fitzgibbon, 1997) and warren-site suitability (Cowan, 1991). As a result, the impact of foxes on nest success may be expected to vary between sites. There is evidence to suggest that fox predation on adult gamebirds varies with main prey abundance: in Scottish moorlands, Leckie *et al.* (1998) found that the occurrence of adult gamebirds in fox scats was negatively related to the abundance of rodents and not the abundance of gamebirds themselves. Although many studies in northern latitudes have detected switches in fox diet from small mammals to gamebirds and their nests during temporal drops in rodent abundance (e.g. Angelstam *et al.*, 1984), no studies have attempted to detect differences in nest predation due to spatial variation in main prey abundance. There are two possible reasons for this: 1) spatial differences in rodent abundance in more southern latitudes are not as dramatic as temporal cyclical changes in rodent abundance in northern latitudes, and therefore not considered as important; and 2) the larger variety of alternative prey types in more southern habitats makes it incredibly difficult to measure the relative abundance of all prey types between sites. Clearly, more empirical work must be carried out to determine the effect of relative prey abundance on nest predation by foxes.

In some respects, foxes are a useful model animal for studying the effect of habitat changes on vertebrate predator-prey interactions because a) they are very common and live in a wide variety of habitats; b) they appear to exhibit a wide range of contrasting

foraging strategies, ranging from sit-and-wait ambush tactics to extensive systematic search tactics; c) their diet can be estimated relatively easily by scat analysis; and d) the results of such a study may lead to recommendations for management of nest predation. However, in other respects, fox predator-prey systems are very unwieldy and difficult to study in practice, because of a) the difficulty in estimating fox abundance and activity, which requires trapping and radio-tracking; and b) the difficulty in measuring relative prey abundance at different sites. Estimating the relative abundance of fox prey in British farmland, would at the very least, require small mammal trapping to measure rodent abundance, and nocturnal spotlight counts or active warren entrance counts to measure rabbit abundance, making the field work labour intensive and potentially expensive. In addition, any study measuring the effect of foxes on nest success would need to include a method of reliably identifying predators, such as infra-red activated, automatically forwarding remote cameras at nest sites.

A better understanding of the factors influencing the foraging behaviour of red foxes may lead to a more scientific approach to the management of predation. The potential to manage nest predation by habitat and alternative prey management may be attractive to some reserve managers, particularly if the establishment of such practises leads to a long-lasting and low maintenance method of reducing nest predation.

8. References

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